The Updated Late Miocene Large Mammal Fauna from Samburu Hills, Northern Kenya

AUTHOR(S):

TSUJIKAWA, Hiroshi

CITATION:

TSUJIKAWA, Hiroshi. The Updated Late Miocene Large Mammal Fauna from Samburu Hills, Northern Kenya. African study monographs. Supplementary issue 2005, 32: 1-50

ISSUE DATE:

2005-12

URL:

https://doi.org/10.14989/68471

African Study Monographs, Suppl., 32: 1-50, December 2005

THE UPDATED LATE MIOCENE LARGE MAMMAL FAUNA FROM SAMBURU HILLS, NORTHERN KENYA

Hiroshi TSUJIKAWA
Graduate School of Science, Kyoto University

ABSTRACT The Late Miocene Fauna from the Namurungule Formation, Samburu Hills, Northern Kenya was described by Nakaya (1994) and Nakaya *et al*. (1984, 1987) based on the 1982 and 1984 collections. Since then, numerous fossils were collected during the 1986, 1998 and 1999 field seasons. The additional large mammal fossil specimens which are described in this paper include Amphicyonidae or Ursidae gen. et sp. indet., Machairodontinae gen. et sp. indet., Felidae gen. et sp. indet., *Choerolophodon* sp., *Deinotherium* sp., Pliohyracidae gen. et sp. indet., *Hipparion africanum*, *Paradiceros mukirii*, *Chilotheridium pattersoni*, *Nyanzachoerus* sp. small (*N.* cf. *devauxi*), *Nyanzachoerus* sp. large, *Kenyapotamus coryndoni*, *Palaeotragus* cf. *germaini*, Boselaphini sp. large (*Tragoportax* sp.), Boselaphini sp. small (gen. et sp. nov.), Reduncini gen. et sp. indet., *Gazella* sp. and Bovidae gen. et sp. indet.

Choerolophodon sp., Pliohyracidae gen. et sp. indet. and Reduncini gen. et sp. indet. were new discoveries in the Namurungule Formation. *Nyanzachoerus* sp. small (*N.* cf. *devauxi*), *Palaeotragus* cf. *germaini* and Boselaphini sp. large (*Tragoportax* sp.) were revised on the basis of well preserved new material. According to the updated faunal list, the Namurungule Fauna shows strong resemblance to faunas of East African localities of the same period, early Late Miocene (10.5 - 9.0 Ma), but shows strong difference from the faunas of East African localities of the Middle (older than 10.5 Ma) and late Late Miocene (7.0 - 5.5 Ma).

Key Words: Late Miocene; Large mammal fauna; Northern Kenya.

INTRODUCTION

The Late Miocene is an important epoch for understanding human and mammal evolution in East Africa. In palaeoanthropology, bipedalism which is one of the features that distinguish the hominids from other hominoids is thought to have evolved in East Africa around 8-7 Ma (Coppens, 1994). To test the hypothesis, it is necessary to find hominid or hominoid fossil remains from this period. However, there is a paucity of hominid and hominoid fossil remains between the Middle to Latest Miocene in East Africa. In the Middle Miocene, many hominoid fossil remains have been discovered. *Kenyapithecus africanus*, *K. wickeri*, *Nacholapithecus kerioi* were collected from the Maboko, Aka Aiteputh and Fort Ternan Formations, Kenya (e.g. Ishida *et al.*, 1999; Leakey, 1962; Le Gros Clark & Leakey, 1951; Ward *et al.*, 1999). The Latest Miocene hominid, *Orrorin tugenensis* was collected from the Lukeino Formation (ca. 6 Ma), Kenya (Senut *et al.*, 2001) and *Sahelanthropus tchadensis* was collected from Toros-Menalla site 266 (6 - 7 Ma), Chad (Brunet *et al.*, 2002). Numerous australopithecine fossils (e.g. *Australopithecus* spp. and *Ardipithecus ramidus*) were collected from sites around 5 Ma (e.g. White *et al.*, 1994). However, there are few Late Miocene fossiliferous localities between 10.5 and 7 Ma in East Africa. In addition, those localities, for example, the Nakali, Ngerngerwa Formations and Member E of the Ngorora Formation, Kenya and the Ch'orora Formation, Middle Awash, Ethiopia, yield few fossil remains and include no hominoids. How-

ever, the Namurungule Formation (ca. 9.5 Ma), Samburu Hills, Northern Kenya yielded a Late Miocene hominoid, *Samburupithecus kiptalami*.

In palaeomammalogy, the Late Miocene in East Africa is important. For example, there is a dearth of bovid fossil remains from the same period. In the Middle Miocene, boselaphines (e.g. *Eotragus* and *Kipsigicerus*) and caprines (e.g. *Gentrytragus* and *Pachytragus*) were relatively dominant in bovid faunas. In the Latest Miocene or Earliest Pliocene, however, bovid faunas completely change. More recent tribes, alcelaphines, tragelaphines and bovines become more dominant. In contrast, most of the boselaphines and caprines disappeared (Gentry, 1990). However, the information on bovids is poor from this period. Similar things happened to the other mammal taxa. The Namurungule Formation yielded numerous mammal fossil remains in comparison with contemporaneous localities in East Africa. The Namurungule Fauna will be important for reconstructing the palaeoenvironment of a Late Miocene hominoid, *S. kiptalami* which is known only by a maxilla.

Since the 1980 field season, the Japan-Kenya Expedition has continued with palaeoanthropological, palaeontological and geological researches in the Sumburu Hills Area, Northern Kenya. During the 1982, 1984, 1986, 1998 and 1999 field seasons, numerous fossils were collected during excavations in the hominoid bearing site, SH 22 and by surface prospecting. The large mammal fauna from the 1982 and 1984 collections was described by Nakaya *et al.* (1984, 1987). A Late Miocene large hominoid, *S. kiptalami*, was collected during the 1982 field season and was described by Ishida & Pickford (1997). The rodent remains, *Paraulacodus* sp. and *Paraphiomys* sp. were described by Kawamura & Nakaya (1984, 1987). Furthermore, a footprint fauna consisting of aves, carnivores, rhinocerotids and artiodactyls at site SH 23 was described by Nakano *et al.* (2001). Nakaya (1994) summarized the Namurungule Fauna of the 1982 to 1986 collections. In this paper, large mammal specimens of the 1986, 1998 and 1999 collections are described (Table 1) and the Namurungule Fauna is updated.

Geography

The Samburu Hills Area is situated on the eastern margin of the Gregory Rift Valley, Northern Kenya, about 500 km north from Nairobi and about 30 km west of Baragoi Town, Samburu District (Sawada *et al.*, 1987). The Samburu Hills form a belt about 30 km wide and about 80 km long trending in a north-south direction forming the eastern wall of the Suguta Valley (Nakaya, 1994).

Geology

The Namurungule Formation consists mainly of mudstone, sandstone, and gravel intercalated with beds of mud flow deposits and tuff. The Namurungule Formation overlies the Aka Aiteputh Formation and is covered by the Kongia Formation in the Samburu Hills area (Sawada *et al.*, 1998).

Eighty-four fossiliferous sites were known there until the end of the 1999 field season (Ishida *et al*., 2001). The age of the Namurungule Formation was determined as 9.5 Ma by K-Ar dating (Sawada *et al.*, 1998) and was correlated with Faunal Set VI (7.5 - 10.5 Ma) of Pickford (1981) on the basis of the faunal assemblage (Pickford *et al*., 1984b).

The Namurungule Formation is divided into two members (upper and lower) by the mud flow deposits situated in the middle of the formation. The Lower Member is mudstone and

Table 1. Mammals of the Namurungule Formation from the 1986, 1998 and 1999 collections.

Order	Family	Gen. et sp.	Member
Carnivora	Amphicyonidae or Ursidae	gen. et sp. indet.	?
	Felidae	Machairodontinae indet.	?
Proboscidea	Gomphotheriidae	*Choerolophodon* sp.	L
	Deinotheriidae	*Deinotherium* cf. *giganteum*	L
Hyracoidea	cf. Pliohyracidae	gen. et sp. indet.	L
Perissodactyla	Equidae	*Hipparion africanum*	L, U
	Rhinocerotidae	*Paradiceros mukirii*	L
		Chilotheridium pattersoni	L
Artiodactyla	Suidae	*Nyanzachoerus* sp. small (*N.* cf. *devauxi*)	L, U
		Nyanzachoerus sp. large	?
	Hippopotamidae	*Kenyapotamus coryndoni*	L
	Giraffidae	*Palaeotragus* cf. *germaini*	L, U
		? *Samotherium* sp.	U
	Bovidae	Boselaphini sp. large (*Tragoportax* sp.)	L
		Boselaphini sp. small (gen. et sp. nov.)	L
		Reduncini gen. et sp. indet.	?
		Gazella sp.	?
		Bovidae gen. et sp. indet.	?

L: Lower Member; U: Upper Member.

includes localities: SH 8, 9, 20 - 24, 27, 34, 50 - 54, 59 and 61 - 63. The Upper Member consists of a mudstone-dominant part and a brown-colored conglomerate part which are interdigitated. The Upper Member with fine lithology includes localities: SH 4, 5, and 28 and the conglomerate (coarse facies) part includes localities: SH 11 - 16, 19, 25, 38 and 41 (Pickford *et al*., 1984a, 1984b). In addition, SH 6, 17, 31, 45 - 46 belong to the uppermost part of the underlying Aka Aiteputh Formation. This part was dated as being younger than 9.9 Ma and older than 9.6 Ma by K-Ar dating method (Sawada *et al.*, 1998). However, the positions of new fossiliferous sites, SH 65 - 84, are unknown.

MATERIALS

The quantities of each mammal taxon collected in each site during the 1986 to 1999 field seasons are given in Table 2. All the fossil materials from the Namurungule Formation are stored at the National Museums of Kenya. These materials are compared with Middle and Late Miocene large mammals from Sub-Saharan Africa, North Africa, Sub-Paratethys and the Siwaliks. They are housed at the National Museums of Kenya (Nairobi), British Museum (Natural History)(London) and Laboratoire de Paléontologie et Vertébrés et de Paléontologie Humaine, Université de Paris VI .

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family Amphicyonidae Haeckel, 1866 or Ursidae Fischer de Waldheim, 1817
gen. et sp. indet.
(Figs. 1A-D)

Table 2. Quantity of the new specimens by taxon and site during the 1986, 1998 and 1999 field seasons.

Locality \ Taxon	Rodentia	Carnivora	Proboscidea	Hyracoidea	Equidae	Rhinocerotidae	Suidae	Hippopotamidae	Giraffidae	Bovidae	Total
SH 8	-	-	-	-	1	-	-	-	-	-	1
SH 9	-	1	-	-	2	3	-	-	8	5	19
SH 22	-	-	-	1	3	6	1	1	6	3	21
SH 23	1	-	-	-	2	-	1	-	-	2	6
SH 24	-	-	-	-	1	-	-	-	-	-	1
SH 26	-	-	3	-	-	-	-	-	-	-	3
SH 32	-	-	-	-	-	-	-	-	3	1	4
SH 33	-	-	-	-	-	-	-	-	1	-	1
SH 39	-	-	-	-	1	-	-	-	-	-	1
SH 51	-	-	1	-	-	-	-	-	-	-	1
SH 52	-	-	-	-	2	-	-	-	-	-	2
SH 61	-	-	-	-	-	-	-	-	-	1	1
SH 62	-	-	1	3	-	1	-	-	1	2	8
SH 65	-	-	-	-	-	4	-	-	-	-	4
SH 66	-	-	-	-	4	1	5	-	8	-	18
SH 67	-	-	-	-	3	-	-	-	-	-	3
SH 68	-	-	-	-	-	1	-	-	-	-	1
SH 69	-	1	1	-	6	4	1	-	8	1	22
SH 70	-	-	-	-	-	-	-	-	-	1	1
SH 71	-	-	-	-	-	1	-	-	-	-	1
SH 72	-	-	-	-	1	-	2	-	-	1	4
SH 73	-	-	-	-	-	1	1	-	2	1	5
SH 74	-	-	-	-	1	-	-	-	1	1	3
SH 75	-	-	-	-	4	1	5	-	-	2	12
SH 76	-	1	-	-	6	1	-	-	4	1	13
SH 77	-	-	-	-	-	-	-	-	1	-	1
SH 78	1	-	-	-	3	2	-	-	1	1	8
SH 79	-	-	-	-	-	-	-	-	-	1	1
SH 80	-	-	1	-	-	-	-	-	-	-	1
SH 81	-	-	-	-	3	-	-	2	-	-	5
SH 82	-	-	-	-	-	-	1	-	-	-	1
SH 84	-	-	1	-	-	2	-	-	-	-	3
Total	2	3	8	4	43	28	17	3	44	24	176

Material: Right mandible with P_4 (KNM-SH 37914, loc. SH 76), right mandible with M_2 (KNM-SH 37907, loc. SH 76)
Horizon: Unknown Member of the Namurungle Formation

Description

Two pieces of the right mandibular body, KNM-SH 37907 and 37914, were collected from SH 76 during the 1998 field season. These two specimens are from the same individual. KNM-SH 37914 includes the erupting P_4 and KNM-SH 37907 has the M_2, an alveolar margin of M_3 and a partial masseteric fossa. These specimens indicate a young individual because these cheek teeth are in the process of erupting.

P_4 which is slightly worn at the tip of the protoconid, is triangular in buccal and lingual views. The protoconid is positioned almost in the middle of the crown. The

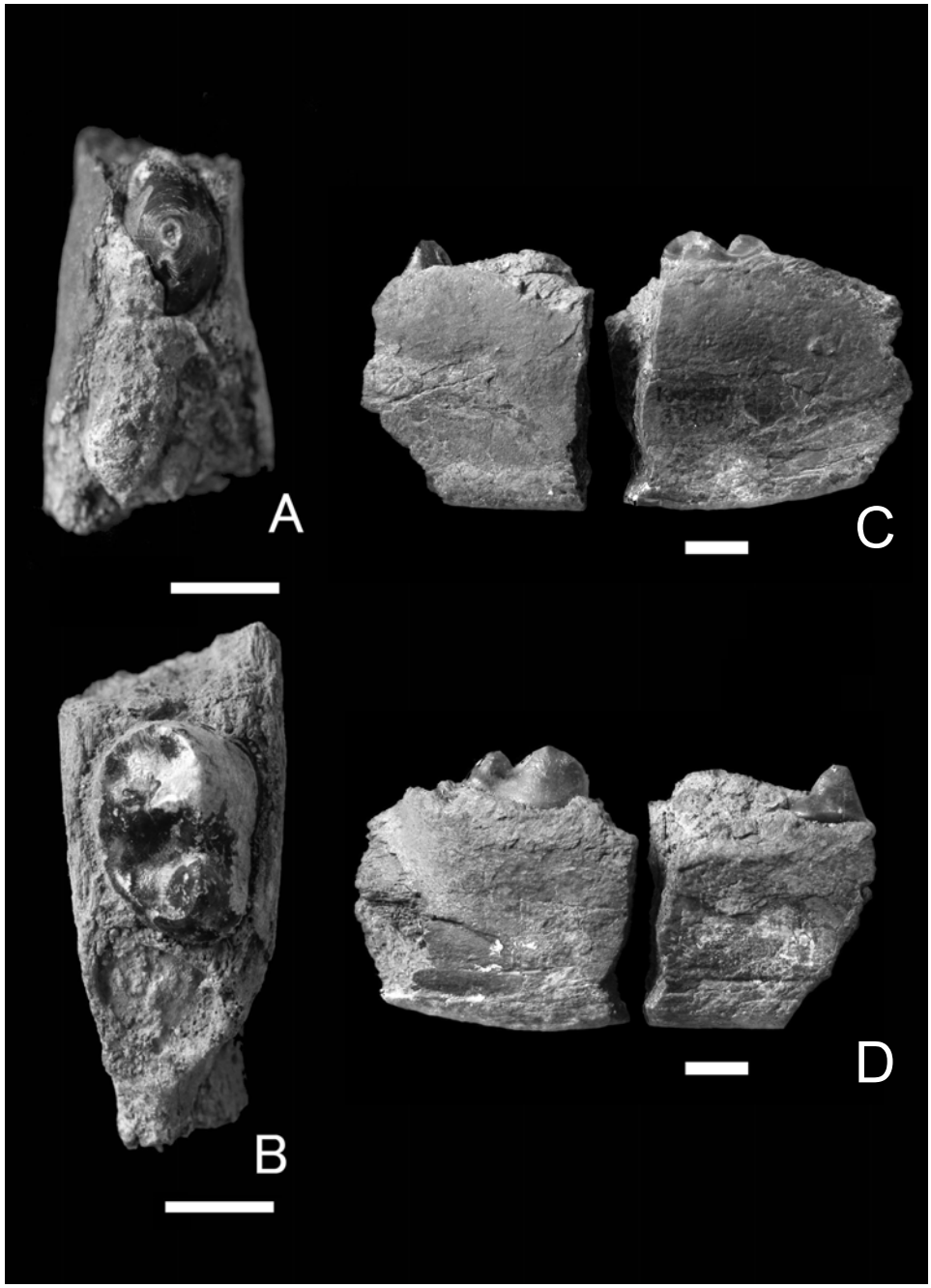

Fig. 1. A-C: Amphicyonidae or Ursidae gen. et sp. indet. A) occlusal view of the right P_4 (KNM-SH 37914); B) occlusal view of the right M_2 (KNM-SH 37907); C) buccal view of the right mandible fragments (KNM-SH 37907 & 37914); D) lingual view of the right mandible fragments (KNM-SH 37907 & 37914). Scales in cm.

Table 3. Measurements (mm) of the M_2 of Miocene amphicyonids and ursids of Africa (Ginsburg, 1977a; Howell, 1987; Savage, 1965; Schmidt-Kittler, 1987).

		Length (L)			Breadth (Br)			L/Br	
Taxon	N	min	max	ave	min	max	ave	min	max
(SH 37907)	1	20.2	20.2	20.2	16.4	16.4	16.4	1.23	1.23
C. euryodon	4	13.7	15.2	14.2	9.1	11.1	10.1	1.33	1.53
Agr. africanum	7	28.6	34.0	30.9	21.9	26.0	23.9	1.21	1.40
Agriotherium spp.	13	26.0	34.2	30.8	20.0	26.0	23.5	1.21	1.40
Agn. cf. *antiquum*	1	18.7	18.7	18.7	13.8	13.8	13.8	1.09	1.09
Indarctos spp.	18	22.0	32.4	26.9	15.6	23.3	19.0	1.28	1.50

N: number of specimens; min: minimum; max: maximum; ave: average.

anterior and posterior sides are swollen but have no cuspids. The cristid runs posteriorly from the protoconid. Measurements of the P_4 are 15.3 mm in length, about 9.5 mm in breadth and 9.1 mm in height. M_1 is not available. M_2 is oval to trapezoidal in outline and in occlusal view its buccal edge is longer than the lingual one. The trigonid basin is smaller and shallower than the talonid one. The protoconid is the highest cuspid in the crown. The hypoconid is the second highest. The paraconid is fairly weak and low. The metaconid is low and is placed slightly more posteriorly than the protoconid and more medially than the paraconid. The anterior cristid runs from the protoconid to the anterior margin of the crown then to the lingual side slightly beyond the paraconid. Another posterior cristid descends to the valley between the protoconid and hypoconid then rises to the hypoconid and descends again to the posterior margin of the crown then curves antero-lingually. Measurements of the M_2 are 20.2 mm in length, 16.4 mm in breadth and 10.6 mm in height. The alveolar margin of M_3 shows reduced size and a subcircular occlusal line. The lingual surface of the mandibular body is flat. Measurements of the alveolar margin of the M_3 are 11.3 mm in length and 10.6 mm in breadth. The posterior part of the masseteric fossa is broken posterioly, but the anterior part extends to the level of the posterior margin of M_3.

The cheek teeth of KNM-SH 37907 and 37914 are similar to those of amphicyonids and ursids. The specimens, especially the M_2, are briefly compared with several species of amphicyonid and ursid.

The Early Miocene amphicyonid, *Cynelos euryodon* was relatively common in Eastern Africa (Savage, 1965; Schmidt-Kittler, 1987). However, *C. euryodon* is much smaller than KNM-SH 37907 in M_2 size (Table 3). The length is 70 % and the breadth is 60 % of the Namurungule specimen. Furthermore the M_2 is less compressed bucco-lingually than that of KNM-SH 37907 in the Length/Breadth index (L/Br) (Howell, 1987).

During the Late Miocene and Pliocene, several amphicyonids and ursids were present in North and South Africa. For example, several M_2s of the Pliocene ursid from Langebaanweg, *Agriotherium africanum* are available (Howell, 1987). However, *Agr. africanum* is much larger than KNM-SH 37907 in M_2 size. The length and breadth are around 150 % of the Namurungule specimen. Even the smallest M_2 of *Agr. africanum* is much larger. The other species of *Agriotherium* are also larger (Howell, 1987). M_2 of the Early Pliocene ursid, *Indarctos* sp. from the Sahabi Formation, Libya, is available for comparison (Howell, 1987). The Sahabi *Indarctos* is also much larger than KNM-SH 37907. The length is 145 % and the breadth is 130 % of the Namurungule specimen. The L/Br index is larger and the Sahabi M_2 is more compressed bucco-lingually. Howell (1987) compared

the M_2 with *Indarctos* species from Eurasia and North Africa. The sizes of M_2 of *Indarctos* species are variable within the genera. However, all of them are larger than KNM-SH 37907. In addition, the L/Br indices also larger in all the lower second molars.

M_2 of the Late Miocene amphicyonid, *Agnotherium* cf. *antiquum* from the Beni Mellal Formation, Morocco, is available (Ginsburg, 1977a). *Agn.* cf. *antiquum* is slightly smaller than KNM-SH 37907, but its L/Br index is larger. However, the occlusal morphology is similar to that in the illustration provided by Ginsburg (1977a).

Thus, KNM-SH 37907 and 37914 are more likely to belong to *Agnotherium* rather than to *Cynelos*, *Agriotherium* or *Indarctos*.

Family Felidae Gray, 1825
Subfamily Machairodontinae Gill, 1872
gen. et sp. indet.
(Figs. 2A-C)

Material: Skull (KNM-SH 17991, loc. SH 69)
Horizon: Unknown Member of the Namurungule Formation

Description

KNM-SH 17991 is a well-preserved skull of an old individual, the cheek teeth of which are almost worn out. The zygomatic arches are partly broken, as are the sagittal crest, the zygomatic process of the frontals, the external occipital protuberance, the left occipital condyle, the superior nuchal lines and the upper dentition and posterior region of the palatine. The upper incisors are completely broken. Only the alveoli are preserved. The left upper canine is missing its tip. The preserved height is about 13 mm from the alveolus. The right upper canine is broken at its base. On the left side, worn P^3 and broken P^4 are preserved. On the right side, only a broken P^4 is preserved in the maxilla. In the frontal surface, four circular to oval equally spaced homodont bite marks are clearly visible, possibly made by a crocodile.

The infraorbital foramen is positioned above and slightly in front of the anterior margin of P^4. The deep infraorbital groove runs with slight curvature antero-ventrally to the C-P diastema. The premaxillae are not in contact with the frontals. The anterior part of the nasals is directed upwards and is slightly wider than the posterior part. The posterior part near the border with the frontals is slightly depressed. The ventral surface of the palatines is almost flat. However, it has shallow lateral grooves from I^3 to P^4 and two deep antero-posteriorly running depressions on the medial side of the left P^4. The transverse suture between the horizontal plate of the palatine and the palatine process of the maxilla runs at the level of P^3. The median suture in the horizontal palate is fused and forms a weak median crest. Two incisive canals open behind the I^1.

The orbital region starts above the anterior part of P^4. The lachrymal canal opens at the anterior outer margin of the orbit.

In lateral view, the external auditory meatus is positioned slightly above the level of the glenoid cavity and slightly below the level of the hard palate. The postglenoid process is slightly angled anteriorly. The mastoid process is small and is positioned at the same level as the lateral side of the auditory bulla. The auditory bulla is pointed posterolaterally. The basioccipital has a faint median ridge around flat and narrow muscular tuberosities which are poorly developed.

Table 4. Measurements (mm) of the canine of Machairodontinae species from the Late Miocene of Africa (Hendey, 1974).

Specimen	Taxon	Length (L)	Breadth (Br)	Br/L
SH 17991 (left)		18.5	9.8	0.53
SH 17991 (right)		ca.20	ca.10	0.50
L 20505	*Machairodus*. sp.	24.2	11.1	0.46
L 11846	cf. *Homotherium* sp.	35.0	13.5	0.39
M 8280	*Homotherium* sp.	34.3	14.0	0.41

L 20505 and L 11846 are from Langebaanweg, M 8280 is from Makapansgat.

The alveolar margin is only preserved along the incisors. The incisors are aligned parabolically. There are small diastema between I^3 and canine (ca. 5 mm). The upper canine is strongly compressed bucco-lingually. Measurements of the left upper canine are 18.5 mm in mesio-distal length and 9.8 mm in bucco-lingual breadth. The right canine is broken. Measurements of the alveolar margin are about 20 mm in antero-posterior length and about 10 mm in bucco-lingual breadth. The Br/L indices are 0.53 for the left canine and 0.5 for the alveolar margin of the right canine. The cross section is an elongated oval. A posterior vertical keel is present. The anterior surface is rounded without a keel. The lingual surface is flatter than the buccal one. P^1 and P^2 are absent. A diastema is present between the canine and P^3. The diastema is about 11.5 mm long. P^3 is small and almost worn out with two roots. Measurements of the left P^3 is at least 11.8 mm in length and at least 5.5 mm in breadth. P^4 is completely broken. The lengths of the alveolar margin are at least 34 mm in the left and 37 mm in the right. M^1 is not available in this specimen.

The strong compression of the upper canine indicates affinities to machairodonts. During the Late Miocene and Pliocene in sub-Saharan Africa, *Machairodus* sp. and cf. *Homotherium* were representatives of the Langebaanweg fauna (Hendey, 1974). The author studied casts of those specimens (L 20505 and L 11846) at the National Museums of Kenya. The Br/L indices of the canine compression show that KNM-SH 17991 is closer to *Machairodus* sp. than to cf. *Homotherium*. The canine of cf. *Homotherium* is much larger and more compressed than the other two. However, *Machairodus kurteni* from Kalmakpai, Kazakhstan has a large and strongly compressed upper canine (Br/L = 0.39) like the Langebaanweg *Homotherium* (Sotonikova, 1992). Thus it is necessary to compare with more specimens.

The bite marks on the frontals are thought to be due to a large reptile, probably a crocodile. Numerous bone and tooth fragments of Crocodylidae gen. et sp. indet. are seen in most fossiliferous sites of the Namurungule Formation (Nakaya, 1994). This fact is informative for the palaeoenvironmental study. KNM-SH 17991 would have been killed near the aquatic environment. Measurements of the canine of Machairodontinae species from the Late Miocene of Africa are given in Table 4.

cf. Felidae gen. et sp. indet.

Material: Left mandible (KNM-SH 38409, loc. SH 9)
Horizon: The Lower Member of the Namurungule Formation

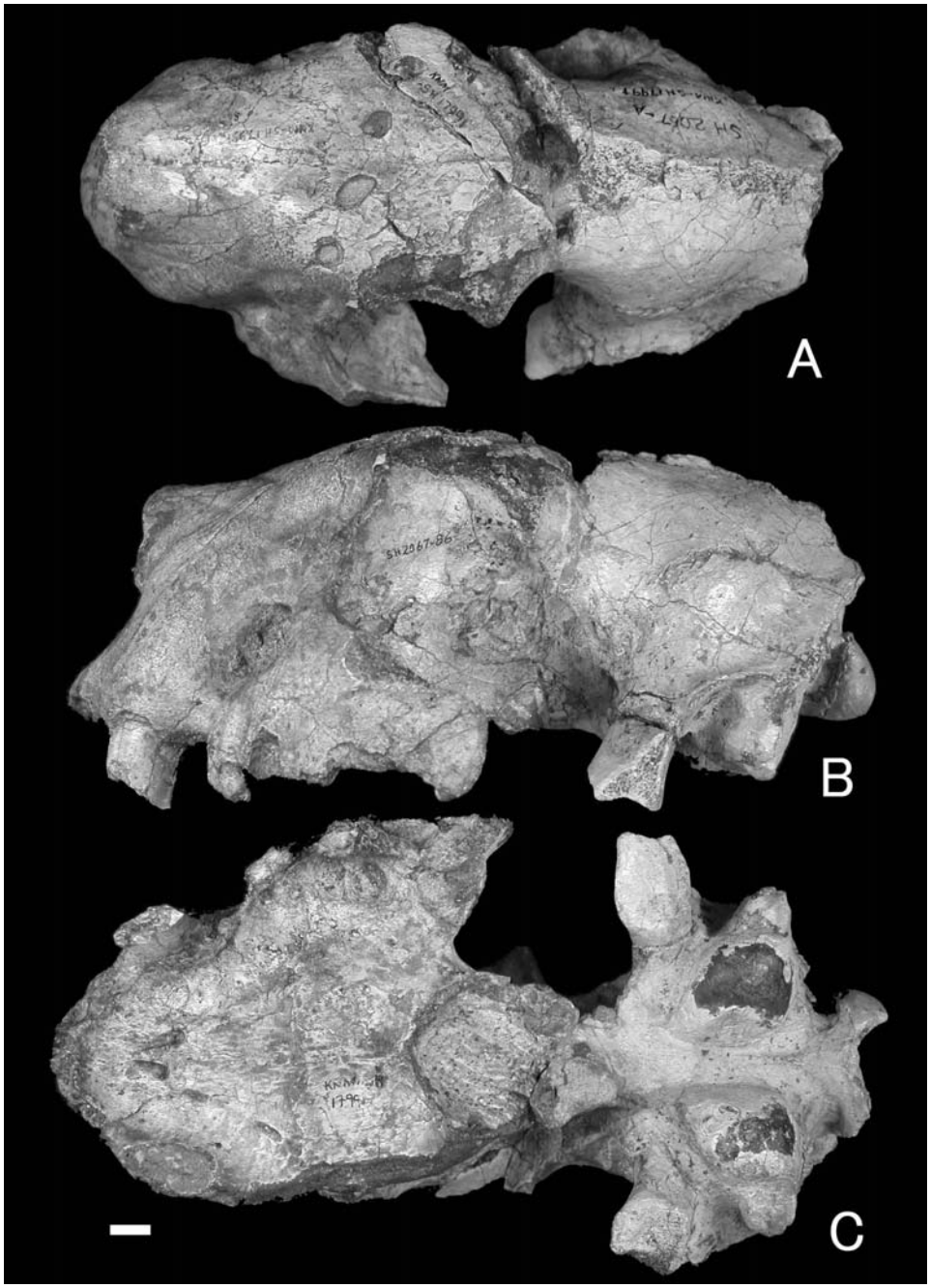

Fig. 2. A-C: Machairodontinae gen. et sp. indet. A) dorsal, B) left lateral and C) ventral view of the skull (KNM-SH 17991). Scale in cm.

Table 5. Measurements (mm) of the P_4 and M_1 of African felids from the Late Miocene and Pliocene (Hendey, 1974).

Specimen	Taxon	Part	Length	Breadth
SH 38409		P_4	(18.4)	(8.2)
		M_1	(23.1)	(9.9)
L 20505	*Machairodus* sp.	M_1	29.0	11.2
L 12641	cf. *Machairodus*	P_4	(20.5)	(9.5)
		M_1	(ca.28)	(11.0)

Measurements of the SH 38409 and L 12641 were taken at the alveolar margin.

Description

The left mandible, KNM-SH 38409 preserves the posterior part of the mandibular body with broken roots of P_4-M_1. However, it lacks the dorsal part of the coronoid process, the posterior part of the mandibular ramus and the anterior part of the mandibular body to P_4. The deep masseteric fossa is similar in shape to that of most felids. The superior margin does not rise straight up. The inferior margin slopes downwards. The anterior margin is positioned at the level of the talonid of M_1 and is slightly higher than the middle of the jaw between the alveolar margin and base of the mandible. The shape of the fossa is triangular. These characters are also seen in many extant felids, including L 20505, *Machairodus* sp. from Langebaanweg, South Africa (Hendey, 1974). The specimen includes broken P_4 and M_1. There are two roots in P_4 and three in M_1. Both crowns are badly damaged.

Compared with L 20505 comprising a left mandible with M_1, KNM-SH 38409 has a lower mandibular body, a slightly smaller M_1 and a less developed masseteric fossa. Measurements of the teeth are given in Table 5. Both P_4 and M_1 are smaller than the specimens of *Machairodus* sp. and cf. *Machairodus* from Langebaanweg, as is the Namurungule machairodont, KNM-SH 17991 (see above).

Order PROBOSCIDEA Illiger, 1811
Family Gomphotheriidae Hay, 1922 (*sensu lato*)
Subfamily Choerolophodontinae Gaziry, 1976
Genus *Choerolophodon* Schlesinger, 1917
Choerolophodon sp.
(Fig. 3A)

Material: Left $M^{1?}$ fragment (KNM-SH 39906, loc. SH 84), left and right M^{2-3} (KNM-SH 38455, loc. SH 26 excavation)
Horizon: The Lower Member of the Namurungule Formation

Description

Left and right upper M^{2-3} (KNM-SH 38455) were excavated *in situ* from SH 26 in the 1998 field season.The M^2 are well worn and fairly weathered because the cementum has almost completely weathered away. The crowns are trilophodont with prominent anterior and posterior cingula in M^2. The M^3 are less worn and the fourth lophs and posterior cingula are missing. The anterior loph is moderately worn, while the second is slightly worn and the third is almost unworn.

In both molars, the second loph is the widest, the first pretrite is positioned slightly to

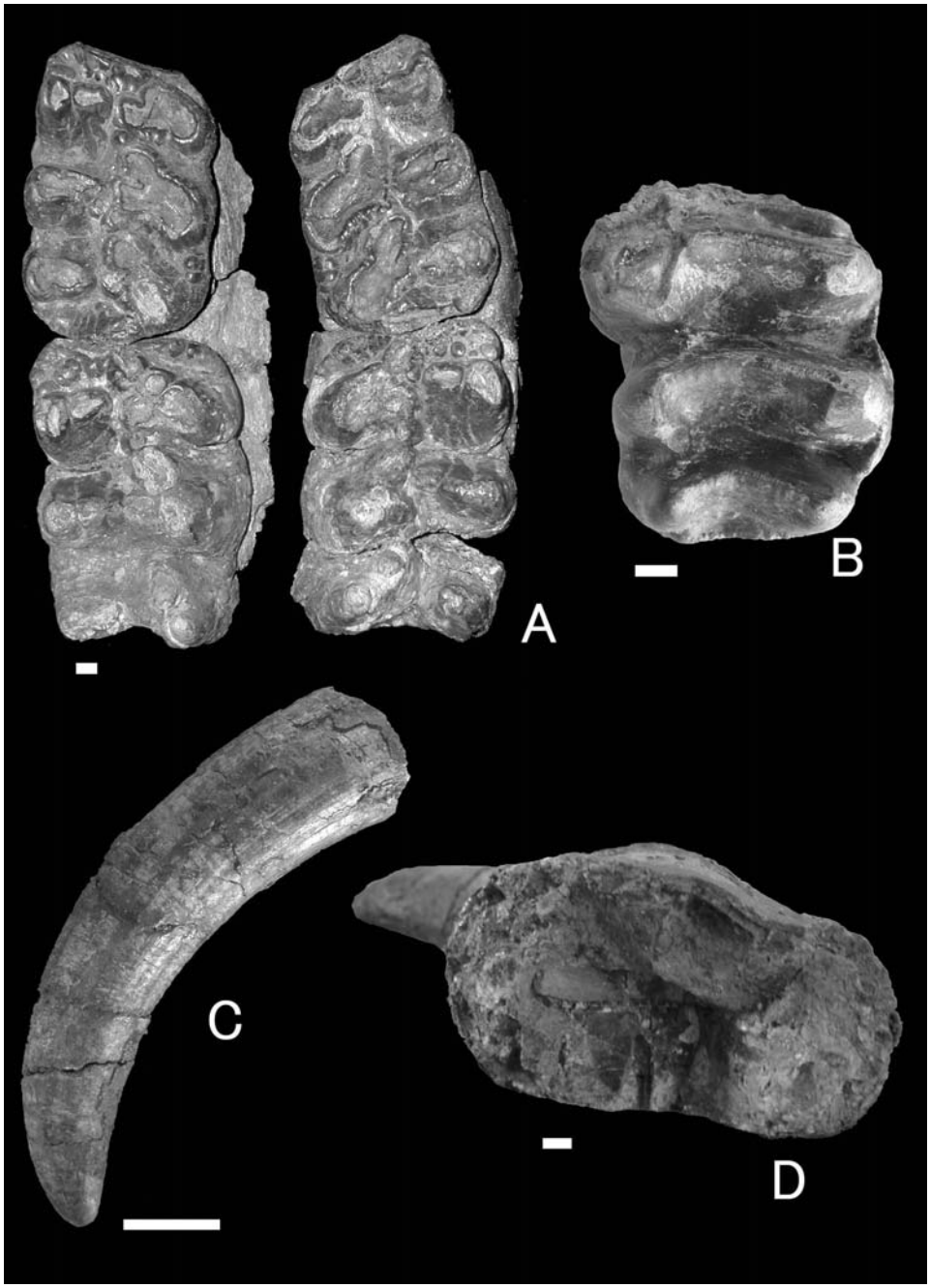

Fig. 3. A: *Choerolophodon* sp. Occlusal view of the left and right M^{2-3} (KNM-SH 38455). **B-D:** *Deinotherium* sp. B) occlusal view of the right M^{1} (KNM-SH 38331A); C) medial view of the right lower tusk (KNM-SH 37913); D) cross section of the proximal end of the right lower tusk (KNM-SH 37913). Scales in cm (A-B and D) and in 10 cm (C).

the rear of the first posttrite and is V-shaped, with the apex of the V pointing slightly posteriorly. The mesocone is fused with the pretrite in M^2 but is only attached in M^3. There is a central conule which blocks the first transverse valley between the first and second pretrites behind the pretrite. The first posttrite has no major conules, creates a zygodont-like crest and is triangular in occlusal view. The second pretrite is also V-shaped, with the apex pointing more posteriorly than the first. It has a well-developed anterior central conule which blocks the first transverse valley with the posterior central conule of the first pretrite. The first transverse valley between the first and second posttrites is wide. The second posttrite has a small conule which blocks the median groove with the mesocone of the second pretrite in the median side and a small posterior central conule in the posterior side. The lingual cingulum between the first and second pretrites is weakly developed. The third pretrite is strongly angled posteriorly. The anterior central conule is positioned fairly anteriorly and blocks the third transverse valley. The mesoconule is fused in the middle of the third pretrite but is hidden in M^3 by the cementum. A lingual cingulum is developed between the second and third pretrites. The transverse valley between the second and third pretrites is moderately wide. The anterior cingulum is well-developed especially on the buccal side. The surface of the cingulum is heavily wrinkled and is fused to the anterior central conule of the pretrite. There are several conules on the buccal side between the anterior cingulum and first pretrite. The posterior cingulum is preserved only in the first molar. It is rugose and fused with the third pretrite on the buccal side.

KNM-SH 39906 is probably a left M^1 fragment with a similar occlusal pattern to KNM-SH 38455. It is fairly worn and weathered. The dentine surrounded by the enamel is missing. The enamel is fairly wrinkled. The antero-posterior length is unknown. However the transverse breadth should be around 55 to 60 mm being slightly smaller than the M^1 of *Choerolophodon* sp. (KNM-NA 4) from Nakali (Tassy, 1986).

Measurements of the upper molar of *Choerolophodon* and *Afrochoerodon* from the Namurungule, Nakali, Ngorora and Fort Ternan Formations are given in Table 6.

Pickford (2001) erected the new genus, *Afrochoerodon* with *A. kisumuensis* and *A. ngorora* from the Middle Miocene. The dental characteristics of the genus are smaller size, less wrinkled enamel, less thick cementum than the Eurasian *Choerolophodon*.

However, he left the Nakali specimens in *Choerolophodon* for their more wrinkled enamel, greater cementodonty and larger size. The Namurungule specimens are similar to the Nakali ones rather than to *A. ngorora* because of those characters. The Namurungule specimens show wrinkled enamel, thick cementum (only in posterior part of M^3). Unfortunately, the measurements of M^2 of *Choerolophodon* sp. and *Afrochoerodon ngorora* in the other localities and the length of M^3 of the Namurungule specimens are not available. However, the Namurungule specimens are larger than *A. ngorora* from Fort Ternan, are probably larger than that from Ngorora and are compatible to *Choerolophodon* from Nakali judging from the specimens in the National Museums of Kenya.

Family Deinotheriidae Bonaparte, 1845
Genus *Deinotherium* Kaup, 1829
Deinotherium sp.
(Figs. 3B-D)

Table 6. Measurements (mm) of the upper molar of *Choerolophodon* sp. and *Afrochoerodon ngorora* from the Namurungule, Nakali, Ngorora and Fort Ternan Formations (Pickford, 2001; Tassy, 1986).

Specimen	Part	Length	Ant. breadth	Mid. breadth	Post. breadth
SH 39906	Left $M^{1?}$	-	-	51.6	-
SH 38455	Left M^2	126.5	76.6	80.6	80.4
	Right M^2	125.2	74.4	78.2	79.1
	Left M^3	140+	90.0	91.0	84.6
	Right M^3	131+	87.7	89.1	83.0
Choerolophodon sp.					
NA 4	Right M^1	81+	-	65+	66+
BN 571 (E)	Left M^2	(98.5)	(68)	(75)	(76)
BN 577 (E)	Right M^3	147.4+	est.83	83	85.4
Afrochoerodon ngorora					
BN 1459 (?)	Left M^2	106	56	(64)	(67)
BN 115 (D)	Left M^3	-	-	80	67
FT 2758	Left M^3	135+	-	75	62+

NA: Nakali; BN: Ngorora (in parenthesis, Member); FT: Fort Ternan.

Material: Skull fragments, and left and right M^{1-2} (KNM-SH 38331A-J, loc. SH 26 excavation), right lower tusk (KNM-SH 37913, loc. SH 26 excavation)
Horizon: The Lower Member of the Namurungule Formation

Description

Skull fragments, teeth and a lower tusk were excavated *in situ* during the 1998 and 1999 field seasons.

The right lower tusk, KNM-SH 37913, is large and massive. The preserved part is long, extending from the alveolar margin to the tip (Fig. 3C). The tusk body is moderately curved downwards and is slight angled laterally. The tip is blunt. The lateral and medial surfaces are slightly indented with shallow grooves running along the curvature of the tusk. However, these grooves do not extend to the tip. No enamel is preserved on the surface. The cross section in the proximal part is oval with lateral and medial depressions being formed by grooves (Fig. 3D).

KNM-SH 38331 consists of skull fragments (suffix G, H and J), right zygomatic arch fragment (I), left M^1 (B), right M^1 (A), protoloph of left M^2 (E), metaloph of left M^2 (D), protoloph of right M^2 (C) and metaloph of right M^2 (F). The isolated left M^1 is well preserved (Fig. 3B). Only the antero-lingual part of the crown is broken. The right M^1 is fairly broken. M^1 shows three lophs. The lophs are slightly curved, the more lingual part from the middle of the loph points slightly anteriorly. Only the protoloph is lightly worn on the apex of the loph. The enamel is thick. The enamel surface is almost smooth, but is slightly wrinkled along the top of the lophs. Small, low and slightly wrinkled anterior and posterior cingula are present. The left and right M^2 are not well preserved, only consisting of fragments. M^2 is comprised of two lophs, the protoloph and metaloph. The anterior and posterior cingula are present, but weak and low. The metaloph is larger than protoloph. Measurements of the tooth are given in Table 7.

Harris (1973, 1978) suggested the size of the tooth as a diagnostic character for distinguishing between the large deinotheres, *Deinotherium* and small deinotheres, *Prodeinotherium*. In his papers, the length (mm) x breadth (mm) of the tooth of *Prodeinotherium* is smaller than 73 x 69 in M^1 and 73 x 75 in M^2 and that of *Deinotherium* is larger than 71 x 64 in M^1 and 70 x 74 in M^2. The size of M^1 and M^2 of KNM-SH 38331

Table 7. Measurements (mm) of teeth of *Deinotheium* cf. *giganteum* (KNM-SH 38331).

Part	Length	Protoloph breadth	Metaloph breadth	Tritoloph breadth
Left M^1	89.3	81+	76.4	62.1
Right M^1	91.9	-	77.1	63.2
Left M^2	ca.83.5	98.4	98.4+	
Right M^2	ca.88	-	-	

is compatible with that of *Deinotherium*. Harris (1978) also suggested the presence and development of the postmetaloph ornamentation of M^2 as a diagnostic character. The postmetaloph is present but reduced in M^2 of KNM-SH 38331. That character also indicates that the specimen likely belongs to *Deinotherium*. In fact, *P. hobleyi* is a small deinothere during the Early to Middle Miocene in Africa while *D. bozasi* is a large deinothere ranging from the Late Miocene to Pleistocene (Harris, 1978). However, Ginsburg & Chevrier (2001) suggested that dental characters in deinotheres from the same localities are variable and the size gradually increases with time. Thus, the presence of two genera of deinotheres is doubtful and all material could be treated as one genus, *Deinotherium*. In addition, it is probable that the supposed generic and specific differences are due to sampling bias. The Late Miocene faunas in Africa are relatively less known than those of the other periods. Thus, the Namurungule specimens are identified as *Deinotherium* sp. and the specific name is left open.

Order HYRACOIDEA Huxley, 1869
Family cf. Pliohyracidae Osborn, 1899
gen. et sp. indet.
(Figs. 4A-C)

Material: Right lower premolar (KNM-SH 37899, loc. SH 22 excavation)
Horizon: The Lower Member of the Namurungule Formation

Description

Terminology of the tooth of Hyracoidea follows Rasmussen & Simons (1988).

A right lower premolar, KNM-SH 37899, was collected from the excavation in SH 22 during the 1998 field season. This specimen is moderately worn and its roots are in a mandibular fragment.

The premolar crown is characterized by its typically double selenodont morphology, molarized with lingual and buccal cingula. The anterior crescent (parastylid - paracristid - protoconid - protocristid - metaconid) is smaller and more curved than the posterior one (metaconid - cristid obliqua - hypoconid - hypocristid - entoconid). The lingual and buccal cingula are well developed. There is no posterior cingulum. The lingual cingulum is long and high, and runs from the parastylid to the entoconid via the metaconid. The buccal one is short and weak, and runs from behind the protoconid to the anterior base of the hypoconid. The metaconid and the parastylid are lightly developed. The small and deep trigonid basin is surrounded by the anterior part of the lingual cingulum and the anterior crescent. The talonid basin is slightly large and shallow, which is closed by the posterior crescent and the extended bases of the metaconid and the entoconid. The buccal valley between the protoconid and the hypoconid is shallow and runs postero-buccally from the

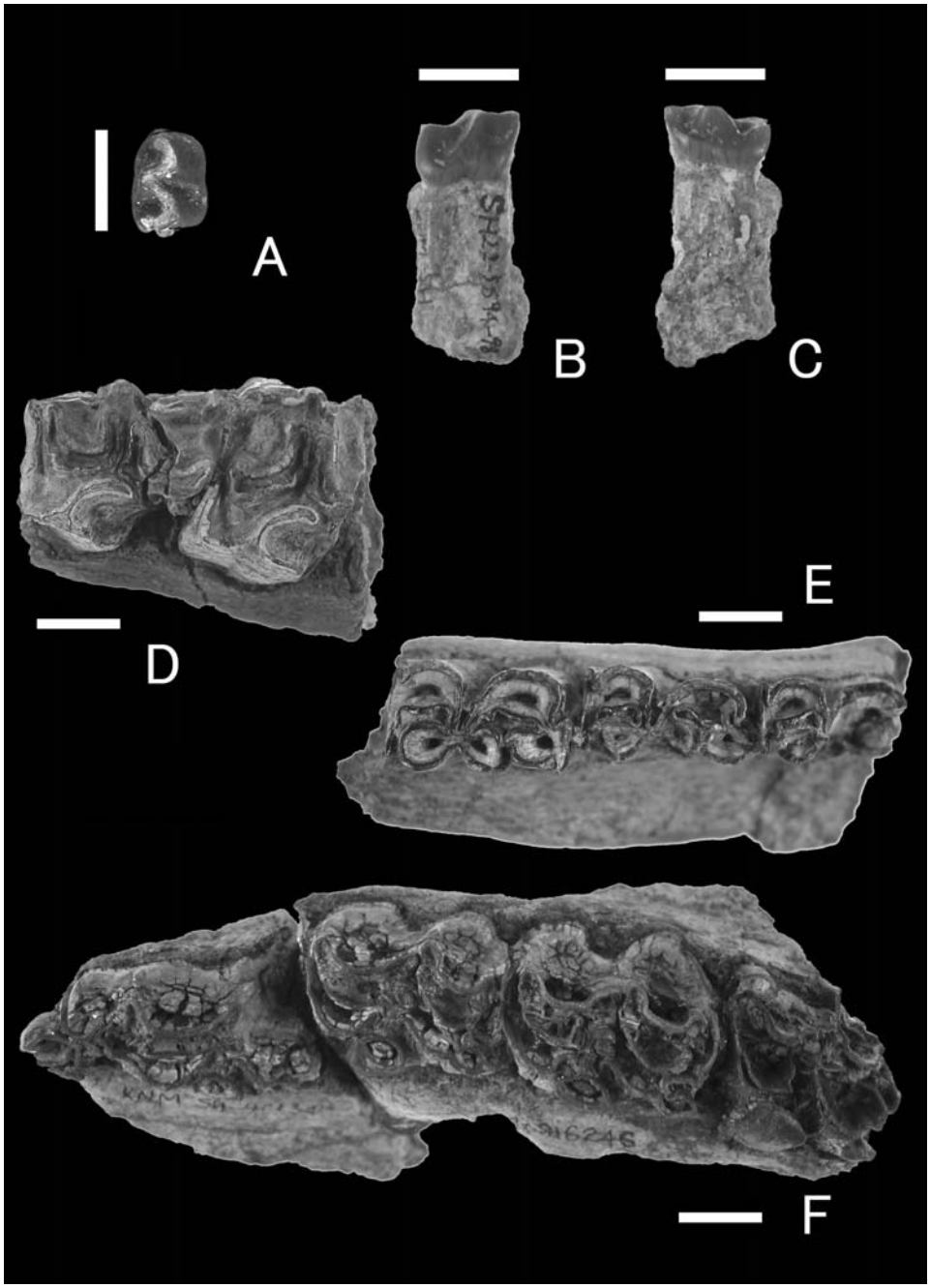

Fig. 4. A-C: cf. Pliohyracidae gen. et sp. indet. A) occlusal, B) buccal and C) lingual views of the right lower premolar (KNM-SH 37899). **D-F:** *Hipparion africanum*. D) occlusal view of the left maxilla with dP^{3-4} (KNM-SH 38426); E) occlusal view of the left maxilla with dP^{1}-M^{1} (KNM-SH 40130); F) occlusal view of the right mandible with P_4-M_2 (KNM-SH 40132). Scales in cm.

metaconid to the base of the hypoconid. A fairly shallow and weak groove runs in the buccal side of the parastylid. Although its roots are not well seen in the mandibular fragment, four roots at least are observed. The Namurungule hyracoid cheek tooth seems to be a well molarized $P_{3 \text{ or } 4}$ close to *Parapliohyrax* in its shape and size. Measurements of the lower premolar are 11.2 mm in length, 8.4 mm in breadth and 7.4 mm in height.

The specimen is the first Hyracoidea from the Namurungule Formation. From the Early to Middle Miocene in East Africa, several taxa of hyracoids, *Brachyhyrax aequatorialis*, *Afrohyrax championi*, and *Meroehyrax bateae*, were described or reviewed by Whitworth (1954), Meyer (1978) and Pickford (2004). However, from the late Middle to Late Miocene in East Africa, only two taxa of hyracoids are described: Fort Ternan, Ngorora and Nakali. From Ngorora, much material of *Parapliohyrax ngororaensis* is known (Pickford & Fischer, 1987). The other pliohyracid species, *P. mirabilis* was described by Ginsburg (1977) and Lavocat (1961) from the Middle Miocene of Beni Mellal, Morroco. However, hyracoid material from Fort Ternan and Nakali are rare and are not given specific or generic names (Pickford & Fischer, 1987). Among the extant genera, *Procavia*, *Heterohyrax* and *Dendrohyrax* are present. (Kingdon, 1997).

All the cheek teeth of the extant African hyracoids, which belong to the family Procaviidae, are much smaller than KNM-SH 37899. In general, the Miocene fossil hyracoids of Africa are much larger than their living relatives.

The P_2 and P_3 of *A. championi* are close to KNM-SH 37899 in their size. However, they differ from KNM-SH 37899 in their greater hypsodonty, more curved cristae, more developed metaconid and entoconid, less developed or no lingual and buccal cingula, larger and deeper trigonid and talonid, deeper valley between protoconid and metaconid extending to the lower level of enamel, more restricted protoconid and hypoconid lobes, and the presence of the posterior cingulum.

All the lower premolars of *Meroehyrax bateae* are smaller than KNM-SH 37899. The M_2 is smaller and the M_3 is larger than KNM-SH 37899.

The lower premolar of the genus *Parapliohyrax* is basically most similar to KNM-SH 37899 with the presence of the well developed lingual cingulum, the slight developed buccal cingulum, the small trigonid and talonid. In size, the M_{2-4} of *P. ngororaensis* are as large as KNM-SH 37899 (Pickford & Fischer, 1987). However, the lower premolar of *P. ngororaensis* differs from KNM-SH 37899 in the less developed lingual cingulum beside the posterior part of the metaconid, the less developed posterior part of the buccal cingulum, the more developed projection of the protoconid, the more columnar cuspids, the deeper valley between the protoconid and hypoconid, the more prominent and lower angled cingular folds.

The P_{2-4} of *P. mirabilis* are also as large as KNM-SH 37899 (Ginsburg, 1977b). However, Pickford & Fischer(1987) did not describe the differences between the lower premolar of *P. ngororaensis* and *P. mirabilis* but the skull characters. The M_3 of the paratype of *P. mirabilis*, studied in a cast in the National Museums of Kenya, is similar to KNM-SH 37899 in size and shape. But it differs by the deeper valley between the protoconid and hypoconid, more columnar protoconid and hypoconid, more curved cristae and weaker and shorter lingual cingulum, deeper trigonid and talonid basins as in *P. ngororaensis*.

The right $P_{2 \text{ or } 3}$ of Procaviidae sp. from Nakali is much smaller than KNM-SH 37899 (5.5 x 3.4 mm). It is much closer to the extant African hyracoids.

In conclusion in size and shape, KNM-SH 37899 is most similar to the lower premo-

lar of *Parapliohyrax*, which belongs to Pliohyracidae, and it differs from the other Hyracoidea from the Miocene of East Africa. However, the Namurungule hyracoid consists of only one specimen. Thus, it is described as cf. Pliohyracidae gen. et sp. indet. pending further comparisons with other pliohyracids such as *Pliohyrax* species from Europe.

Order PERISSODACTYLA Owen, 1848
Family Equidae Gray, 1821
Genus *Hipparion* de Christol, 1832
Hipparion africanum Arambourg, 1959
(Figs. 4D-F)

Material : Right I^3 (KNM-SH 18007 loc. SH 22), left P^2 (KNM-SH 41782 loc. SH 81), left P^3 (KNM-SH 37332 loc. SH 8, 40141 loc. SH 76), right P^3 (KNM-SH 17993, 17995 locality unknown), right P^3, and left $M^{1\text{ or }2}$ (KNM-SH 40144 loc. SH 75), right $P^{4?}$ (KNM-SH 41783 loc. SH 9), left $M^{1\text{ or }2}$ (KNM-SH 38424 loc. SH 76), right $M^{1\text{ or }2}$ (KNM-SH 38437 loc. SH 62), right M^2 (KNM-SH 38423 loc. SH 39), right $M^{2\text{ or }3}$ fragment (KNM-SH 40137 loc. SH 22), left maxilla with dP^1-M^1 (KNM-SH 40130 loc. SH 69), left maxilla with dP^{3-4} (KNM-SH 38426, 39917 loc. SH 76), right $dP^{3\text{ or }4}$ (KNM-SH 38427 loc. SH 67), left upper dP (KNM-SH 40123 loc. SH 78), right upper dP (KNM-SH 38421 loc. SH 67), right upper dP? (KNM-SH 41780, loc. 52), left permanent upper cheek tooth (KNM-SH 40122 loc. SH 78), upper cheek tooth fragment (KNM-SH 40121 loc. SH 66, 41778 loc. 75, 41779 loc. SH 72, 41784 loc. SH 69), left I_1 (KNM-SH 38422 loc. SH 76), right mandible with P_4-M_2 (KNM-SH 40132 loc. SH 78), right mandible with M_{2-3} (KNM-SH 38420 loc. 76), right $M_{2\&3}$ and left $M_{1\&3}$ (KNM-SH 40127 loc. SH 66), left P_2 (KNM-SH 41755 loc. SH 69), left P_3 fragments (KNM-SH 41781 loc. SH 81), left M_1 (KNM-SH 40009 loc. SH 81), left $M_{1\text{ or }2}$ (KNM-SH 38436 loc. SH 62), right $M_{1\text{ or }2}$ (KNM-SH 38438 loc. SH 23), right M_2 (KNM-SH 38425 loc. SH 76)

Horizon : The Lower and Upper Members of the Namurungule Formation

Description

Numerous equid teeth were collected during the 1986, 1998 and 1999 field seasons.

The cheek teeth are hypsodont. The wear of each tooth is variable. In upper cheek teeth: the protocone is separated from the main part of the tooth and is elongated anteroposteriorly. The enamel surrounding the prefossette and postfossette is well wrinkled in the anterior and posterior parts of the fossettes. In lower cheek teeth: the ectostylid is absent and the ptychostylid is weak or absent.

Several cheek teeth show strange characters in comparison with the others.

KNM-SH 38426 is a left maxilla fragment with dP^{3-4} (Fig. 4D). The posterior parts of the protocone in both teeth are broken. The deciduous teeth are fairly worn and have roots. The occlusal surface of the tooth is square or rectangular. The prefossettes and postfossettes are fairly narrow. The enamel surrounding the fossettes is not wrinkled. The protocone is not elongated but round and is connected with the main part of the tooth posteriorly. The enamel lines of the fossettes are fairly simple.

KNM-SH 40130 is left maxilla with dP^1-M^1 (Fig. 4E). The cheek teeth are fairly

Table 8. Measurements (mm) of the teeth of *Hipparion africanum*.

Specimen	Part	Length	Breadth	Height	PL	PB
SH 38422	I_1	10.9	9.2	27.1		
SH 18007	I^3	14.4	7.6	16.0		
SH 40130	dP^1	9.1	9.8	8.5		
	dP^2	31.7+	19.6	10.8+	6.5	4.9
	dP^3	23.7+	22.2	17.3	6.4	4.2
	dP^4	25.2	21.1	14.0	7.3	4.2
SH 38427	$dP^{3 \text{ or } 4}$	27.1	21.0	17.4	6.2	2.9
SH 38421	dP^x	25.0	16.2	41.6	6.1	-
SH 41780	dP^x?	22.0	16.5	44.7	6.7	2.0
SH 39917	dP^x	-	-	-	5.2	5.2
SH 41782	P^2	31.5	20.1+	50.7	7.8	3.9+
SH 17995	P^3	30.3	26.2	65+	9.9	3.7
SH 37332	P^3	25.8+	24.3	31.6+	8.1	5.5
SH 17993	P^3	30.9+	25.1	21.2	8.2	4.5
SH 38426	P^4	26.4	19.2+	9.7	-	-
SH 38426	M^1	-	21.1	6.6	-	-
SH 40130	M^1	ca. 24.5	22.5	12.6	8.5	3.0
SH 38437	$M^{1/2}$	22+	20.8	18.4+	6.6	4.3
SH 38423	M^2	22.3+	20.8+	24.4+	7.1	4.8
SH 39917	P^x or M^x	-	-	-	5.3	5.4
SH 41779	P^x or M^x	-	-	20.8	6.5	4.1
SH 40009	M^1	24.2	22.3	39+	7.4	4.4
SH 40121	P^x or M^x	-	-	14.8	6.8	4.0
SH 40144	P^3	27.1	26.6	50+	8.7	3.7
	$M^{1 \text{ or } 2}$	23.7	25.0	48+	7.0	2.2
SH 41778	P^x or M^x	-	-	-	8.6	6.1
SH 40122	P^x or M^x	27.2	25.6	53.1+	9.3	4.3
SH 40123	dP^x	21.0	22.8	21.8	8.8	5.7
SH 41775	P_2	26.2	12.6	28.8		
SH 38425	M_x	-	12.7	-		
SH 38436	M_x	23.7+	11.8	-		
SH 40127	M_1	20.9	11.0	-		
	M_2	-	9.7	-		
	M_3 (right)	26.0	10.6	-		
	M_3 (left)	25.6	9.9	-		
SH 40132	P_4	23.2	13.4	20.3		
	M_1	21.2	11.7	15.9		
	M_2	20.4	10.8	15.0		
SH 40141	$P_{3?}$	27.0	17.6	50.5		
SH 41783	$P_{4?}$	24.7	15.6	35.1		
SH 38320	M_2	24.1	12.9	29.8		
	M_3	25.2	13.0	16.9		
SH 38438	$M_{1 \text{ or } 2}$	26.1+	14.1	28.4+		

PL=protocone length, PB=protocone breadth.

weathered but unworn. The enamel rises above the dentine and cementum. dP^1 is small and vestigial. The occlusal surface is ovate. The enamel is well wrinkled on the lingual side and less wrinkled on the buccal side. In dP^{2-4}, the protocone is ovate and less elongated than that of M^1. Measurements of the tooth are given in Table 8.

Although *Hipparion* is the most dominant mammal in the Namurungule Formation, most the specimens collected during the recent field seasons are isolated teeth or tooth fragments.

Nakaya (1994), and Nakaya & Watabe (1990) attributed the Namurungule

hipparionines to *H. africanum* on the basis of a well preserved skull, KNM-SH 15683 collected during the 1984 field season (Nakaya *et al.*, 1987), especially because of the morphology of the preorbital fossa and dentition. Furthermore, the Namurungule hipparion has slender proportioned limb bones like *H. africanum* from the Bou Hanifia Formation (Vallesian), Algeria.

Thus, the specimens collected during the recent field seasons probably also belong to *H. africanum*.

Family Rhinocerotidae Owen, 1845
Genus *Paradiceros* Hooijer, 1968
Paradiceros mukirii Hooijer, 1968
(Figs. 5A-B)

Material : Right $P^{3 or 4}$ (KNM-SH 38406 loc. SH 9), right maxilla with P^4 (KNM-SH 37910 loc. SH 73), left M^1 fragment (KNM-SH 17994 loc. locality unknown), left M^2 fragments (KNM-SH 40150 loc. SH 65), left M^3 (KNM-SH 37908 loc. SH 9), right mandible with right P_{2-4} and left P_{2-3} (KNM-SH 37911 loc. SH 68), right mandible with $M_{1 or 2}$ (KNM-SH 37912 loc. SH 65), right mandible with M_{1-2} (KNM-SH 40138 loc. SH 75), left mandible with M_1 (KNM-SH 40143 loc. SH 76), left mandible fragment (KNM-SH 38402 loc. SH 9), left P_3 (KNM-SH 17997, 18000 loc. SH 22), left P_3 fragment (KNM-SH 17996 loc. SH 22), right M_2 (KNM-SH 40120 loc. SH 22), left lower molar fragment (KNM-SH 40134 loc. SH 78), right lower molar fragment (KNM-SH 40139 loc. SH 65), right lower molar fragments (KNM-SH 39913 loc. SH 78)
Horizon : The Lower Member of the Namurungule Formation

Description

Paradiceros is a small rhinocerotid with brachyodont cheek teeth. The protocone is not constricted. The ectoloph is curved. The crista and crochet are well developed. *P. mukirii* is known from the Namurungule Formation (Nakaya, 1994; Nakaya *et al.*, 1984, 1987). Upper and lower dentitions including maxilla and mandible fragments of this species were collected in the recent field seasons.

KNM-SH 37910 is an isolated right P^4 fragment the ectoloph of which is broken. The protocone is weakly constricted. The antecrochet is absent. The strong crochet and small crista are pointed medially. The ectoloph is moderately curved but the buccal part is missing.

KNM-SH 38406 is an isolated left P^4 fragment preserving only the lingual side. It is much more worn than KNM-SH 37910. The enamel pattern in the occlusal surface is different due to the wear but the basic characters are same. The protocone is weakly constricted. The crochet is weakly pointed. The anterior cingulum is present around the anterior side of the protocone.

KNM-SH 37911 is a mandibular symphysis which is comparable to KNM-FT 2869, the paratype of *P. mukirii* from Fort Ternan (Hooijer, 1968). It is slightly deformed in the left side. The size and mandibular depth are as large as the paratype. The symphysis is slightly shorter than KNM-FT 2869. The posterior margin of the symphysis extends to the level of the lingual groove of P_3 whereas it reaches the level of the posterior side of P_3 in the paratype. The cross section of the mandibular body at the posterior margin of P_4 is oval,

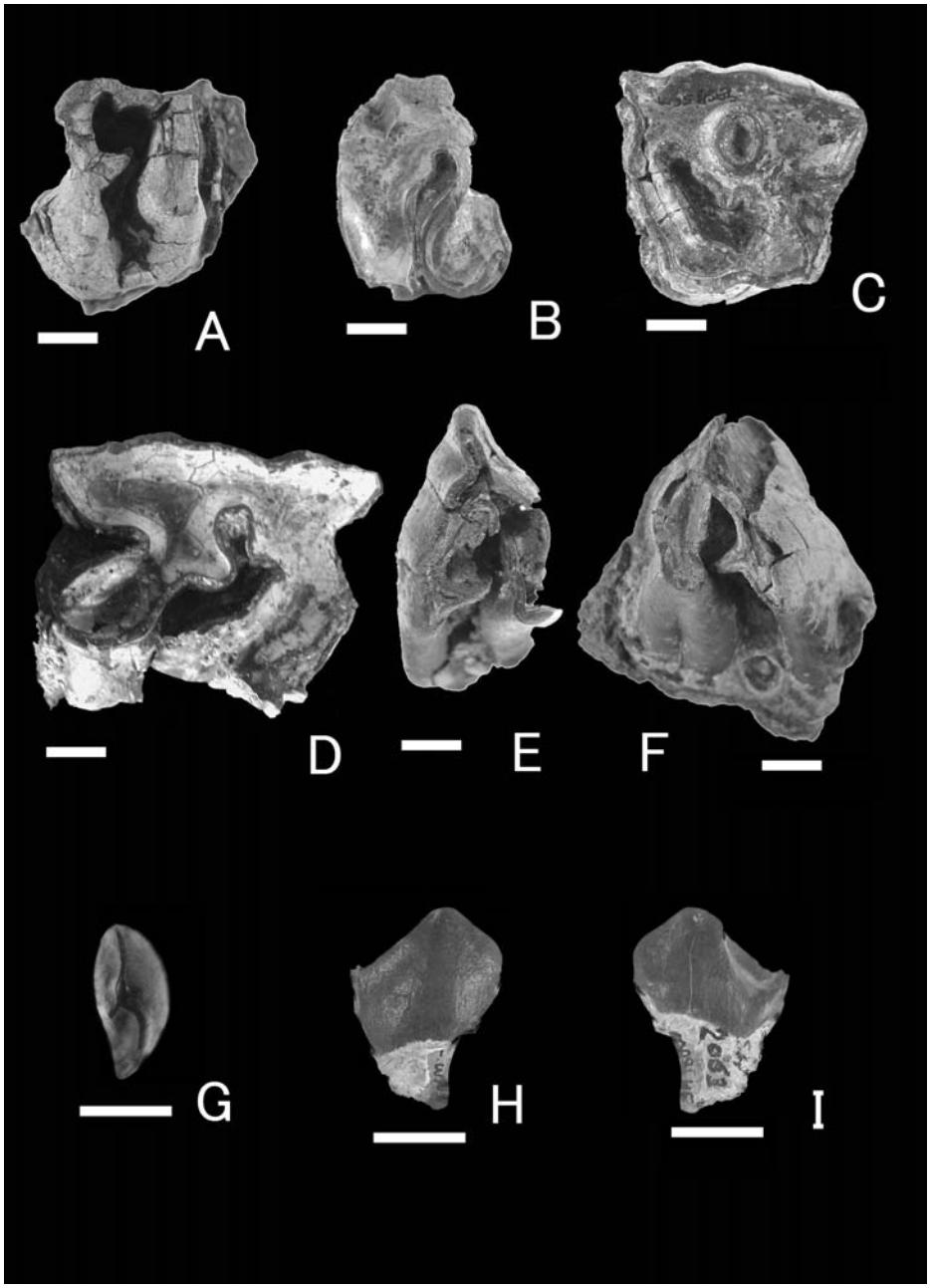

Fig. 5. A-B: *Paradiceros mukirii.* A) occlusal view of the right P^4 (KNM-SH 37910); B) occlusal view of the right P^4 (KNM-SH 38406). **C-F:** *Chilotheridium pattersoni*. C) occlusal view of the left $P^{3 \text{ or } 4}$ (KNM-SH 40128); D) occlusal view of the right M^1 (KNM-SH 40128); E) occlusal view of the right M^3 (KNM-SH 40792); F) occlusal view of the left M^3 (KNM-SH 38404). **G-I:** ? Rhinocerotidae gen. et sp. indet. G) occlusal, H) buccal and I) lingual views of the right $dP_{1?}$ (KNM-SH 38329). Scales in cm.

Table 9. Measurements (mm) of the femora of *Paradiceros mukirii* from the Namurungule and Fort Ternan Formations, Kenya (Hooijer, 1968).

	SH 40136	FT 2720'62	FT 480'62
Greatest length	428	?420	?420
Transverse diameter of caput	75.9	90	-
Proximal width	169.6	170	-
Least width of shaft	52.4	70	70
Greatest distal width	109.7	-	115

its buccal side is flattened and the lingual side is rounded. The symphysis is edentulous. The median length of the symphysis is at least 65 mm. The mental foramina are present, a large one is positioned below the P_2 in the left buccal side and three small ones in the right side. A partial root of P_1 is present in the left side whereas P_1 is absent in the paratype.

KNM-SH 38402 and 40138 are posterior parts of the mandibular body. The jaw is deep and massive, being similar to KNM-FT 2869. The lower cheek teeth are brachyodont.

The genus *Paradiceros* includes only one species, *P. mukirii* (Hooijer, 1968). This genus is reported from the Fort Ternan Formation (Hooijer, 1968) during the late Middle Miocene, Kenya and the Namurungule Formation during the Late Miocene, Kenya (Nakaya, 1994; Nakaya *et al.*, 1987). This rhinocerotid is characterized by its brachyodont cheek teeth, size smaller than *Brachypotherium*, *Aceratherium*, *Dicerorhinus* and *Chilotheridium*, weakly constricted protocone, prominent antecrochet, nasal and frontal horns, subtriangular upper third molars and short humerus and metapodials (Hooijer, 1968). The period of existence of *P. mukirii* is extended to the Late Miocene by its discovery in the Namurungule Formation.

cf. *Paradiceros mukirii* Hooijer, 1968
(Figs. 6A-B)

Material : Right femur (KNM-SH 40136, loc. SH 69), distal fragment of left femur (KNM-SH 40791, loc. SH 69)
Horizon : Unknown Member of the Namurungule Formation

Description

None of the postcranial materials of Rhinocerotidae are associated with dental ones. However, KNM-SH 40136 and 40791 can be compared to femora of *Paradiceros mukirii* from Fort Ternan.

KNM-SH 40136 is an almost complete small right femur. Measurements are given in Table 9. The measurements of this femur indicate that it is fairly close to the Fort Ternan material in size. In greatest length, proximal width and greatest distal width, KNM-SH 40136 shows almost the same value as the two Fort Ternan femora. The transverse diameter of the caput is smaller. In least width of the shaft, it is more slender. The femora of *P. mukirii* are four-fifths as long as that of *Dicerorhinus leakeyi* (Hooijer, 1968). The third trochanter in the Namurungule specimen is positioned higher than in the Fort Ternan sample.

KNM-SH 40791 is a distal part of a femur preserving the lateral condyle. However, it

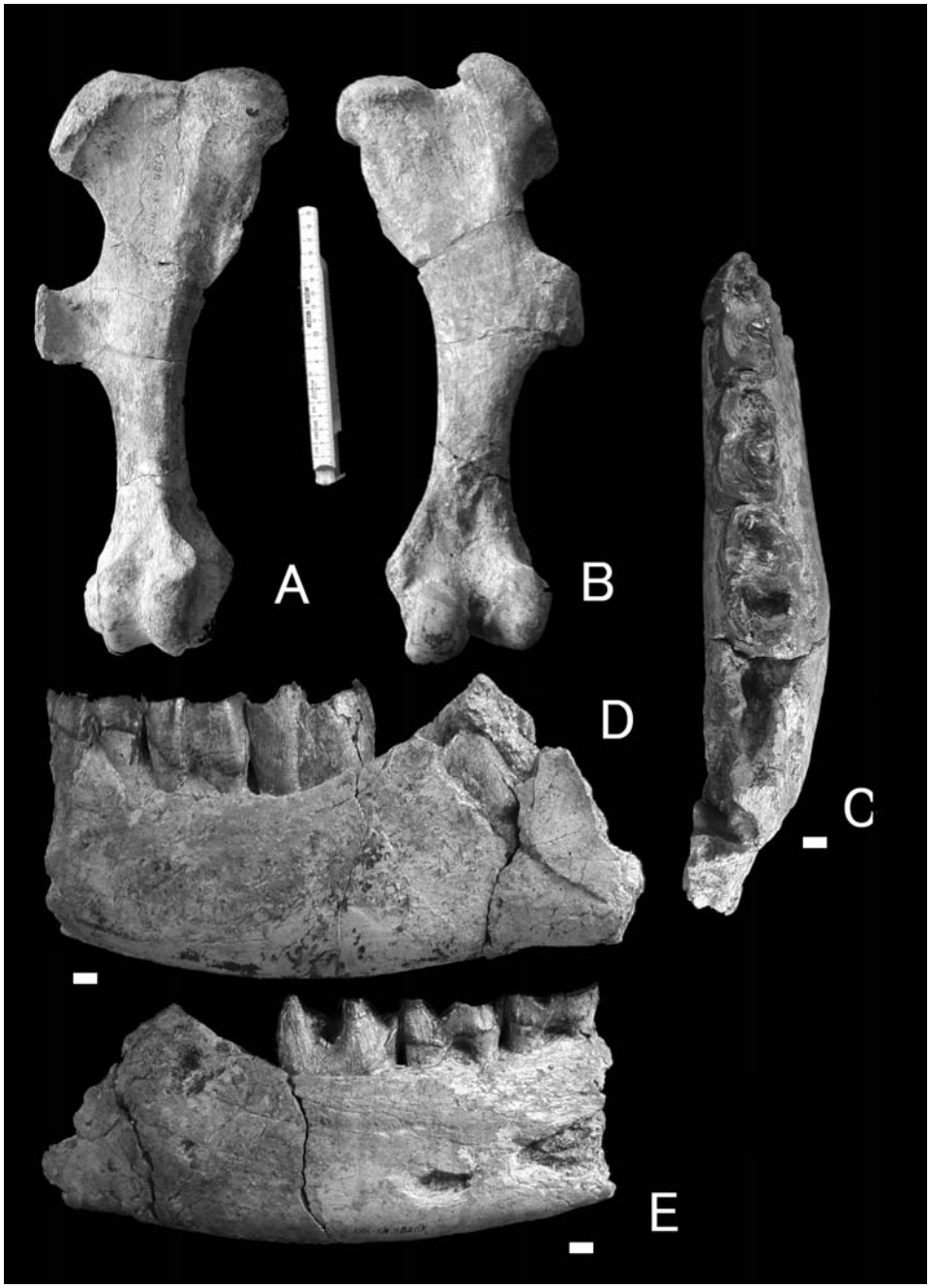

Fig. 6. A-B: cf. *Paradiceros mukirii*. A) dorsal and B) plantar views of the right femur (KNM-SH 40136). **C-E:** *Chilotheridium pattersoni*. C) occlusal, D) buccal and E) lingual views of the left mandible with P_4-M_2 (KNM-SH 38405). Scales in cm (C-E).

is the same size (no measurements available) and comes from the same locality as the specimen described above and it probably belongs to the same individual as KNM-SH 40136.

Genus *Chilotheridium* Hooijer, 1971
Chilotheridium pattersoni Hooijer, 1971
(Figs. 5C-F; 6C-E)

Material : Left $P^{3 or 4}$, M^{1-3} and right M^{1-2} (KNM-SH 40128 loc. SH 84), left M^3 (KNM-SH 38404 loc. SH 66), right M^3 (KNM-SH 40792 loc. SH 84), left mandible with P_4-M_3 (KNM-SH 38405 loc. SH 71)
Horizon : The Lower Member of the Namurungule Formation

Description

C. pattersoni is a large rhinocerotid with hypsodont cheek teeth with a sharply constricted protocone. *C. pattersoni* was previously recorded from the Namurungule Formation by Nakaya (1994) and Nakaya *et al.* (1984, 1987). Several cheek teeth and a mandibular fragment were collected during the recent field seasons.

KNM-SH 40128 is a broken maxilla and several upper cheek tooth fragments. However, an isolated left $P^{3 or 4}$ which is well preserved and a first molar fragment are in comparatively good condition. These specimens indicate a hypsodont rhinocerotid with a strongly constricted protocone and a well developed antecrochet.

The upper $P^{3 or 4}$ is a small hypsodont tooth which is well worn. The protocone and the hypocone are connected by a bridge and the lingual valley between protocone and hypocone is absent. It is possible that the bridge is made by a well developed antecrochet connecting with the hypocone. The bridge encloses a medisinus. The crista is developed mid-lingually in the ectoloph. A crochet is also developed in the metaloph near the ectoloph. The oval medifossette is present in the ectoloph just to the buccal side of the crista. In addtion to the crista and crochet, the lingual line of the ectoloph has several indents. The hypostyle is slightly behind the metaloph. The anterior cingulum extends from the parastyle to the antero-lingual side of the protocone. The weak posterior cingulum extends from the hypocone to the metastyle. The left M^1 preserves a part of the protoloph and ectoloph. It is well worn. The right M^1 preserves the protoloph without protocone and metaloph. The buccal part is concealed by broken maxilla fragments and matrix.

The other materials of KNM-SH 40128 are fragmentary. The left M^{2-3} and right M^2 preserve the buccal part of the tooth crown. The second molars are slightly worn but fairly weathered. The lingual part is broken or missing. The crista is well developed. All the molars lack the protocone. Only one protocone fragment of an upper molar is preserved. It is well worn and shows only the degree of hypsodonty and protocone furchen. KNM-SH 40128 does not reveal precise information about the protocone.

KNM-SH 38404 and 40792 are isolated upper third molars. They are hypsodont teeth. The crown is triangular in occlusal view. The protocone is sharply constricted. The antecrochet is slightly developed. The crochet is well-developed. The hypocone ends sharply on the lingual side. The basal pillar is present between protocone and hypocone on the lingual side. However it is broken in KNM-SH 38404. The anterior cingulum is

Table 10. Measurements (mm) of the teeth of *Chilotheridium pattersoni*.

Specimen	Part	Length	Breadth	Height
SH 40128	Left $P^{3 \text{ or } 4}$	38.6	44.3	37.2
	Right M^1	51.8	-	13.7+
	Left M^2	36.1+	-	60.2+
	Right M^2	55.6	-	42+
	Left M^3	40.3	-	47.5
SH 38404	Left M^3	54.9	65.2	61.6
SH 40792	Right M^3	-	66.9	72.3

present in KNM-SH 38404. Measurements of the teeth are given in Table 10.

? Rhinocerotidae gen. et sp. indet.
(Figs. 5G-I)

Material: Right $dP_{1?}$ (KNM-SH 18004 loc. SH 22)
Horizon: The Lower Member of the Namurungule Formation

Description

KNM-SH 18004 is probably an isolated lower deciduous molar which is almost unworn showing slight wear only in the entoconid area. It is a small and brachyodont tooth. The shape of the crown is elongated antero-posteriorly rather than triangular. The paraconid is not developed and does not branch or make a parastylid. The cristid from protoconid to paraconid is fairly simple, only slightly curved lingually. It has a weakly developed metaconid directed slightly postero-lingually. However the cristid from protoconid to metaconid is fairly short. The entoconid is only slightly developed. The cristid from protoconid to entoconid is fairly simple and slightly curved lingually. It has a hypoconulid without entoconulid branch. Measurements of the teeth are as 17.7 mm in length, 8.4 mm in breadth and 15.4 mm in height.

If the specimen is correctly identified as a rhinocerotid, it is most likely to belong to the genus *Paradiceros* because the specimen shows brachyodont features and the only brachyodont rhinoceros known from the Samburu Hills is *Paradiceros*, the other ones from the Namurungule Formation, *Chilotheridium* and *Kenyatherium* being hypsodont rhinocerotids. *Paradiceros* is the only confirmed rhinocerotid at site SH 22 where the specimen were found.

Order ARTIODACTYLA Owen, 1848
Suborder SUIFORMES Jaeckel, 1911
Family Suidae Gray, 1821
Subfamily Tetraconodontinae Simpson, 1945
Genus *Nyanzachoerus* Leakey, 1958
Nyanzachoerus sp. small (*N.* cf. *devauxi* (Arambourg, 1968))
(Fig. 7A-K)

Material: Left I^2 (KNM-SH 38417 loc. SH 72), left I^2 fragment (KNM-SH 41909 loc. SH 75), right P^4 (KNM-SH 18002 locality unknown), right M^2 (KNM-SH 38049 loc. SH 66), left

mandible with P_{1-4} (KNM-SH 40131 loc. SH 66), left mandible with canine, P_2-M_3 (KNM-SH 40129A loc. SH 66), right mandible with M_{2-3} (KNM-SH 40129B loc. SH 66), right mandible with canine (KNM-SH 40129D loc. SH 66), right mandible with P_4-M_3 (KNM-SH 38051 loc. 69), $P_{3 \text{ or } 4}$ (KNM-SH 37889 loc. SH 73), right M_1 (KNM-SH 40129C loc. SH 69, 41908 loc. SH 75), left M_1 fragment (KNM-SH 41910 loc. SH 75), posterior fragment of right M_1 (KNM-SH 38048 loc. SH 66, 38050 loc. SH 72), right M_2 (KNM-SH 40152 loc. SH 75), molar fragment (KNM-SH 18006 loc. SH 22)

Horizon: The Lower and Upper Members of the Namurungule Formation

Description

Upper and lower teeth and mandibular bodies were collected during the 1986, 1998 and 1999 field seasons. The upper teeth are few, isolated and fragmentary although the lower ones are numerous and some specimens preserve mandibular bodies in good condition and include partial dentitions. The cheek teeth are basically similar to those of the recent *Potamochoerus* but the cusps and cuspids are more columnar like the other *Nyanzachoerus* species (Cooke & Wilkinson, 1978). The terminology for the teeth follows Pickford (1986, 1988).

KNM-SH 38417 is an isolated left I^2 preserving a single root. The tooth is well worn, fairly weathered and massive. The crown is ovate or spindle shaped in occlusal view. The antero-medial part is especially worn. A small accessory cusp is present in the postero-lingual region of the crown.

KNM-SH 18002 is a heavily worn isolated right P^4. The tooth only shows a well developed parastyle and paracone and thick enamel. The occlusal surface is triangular with rounded lingual corners.

KNM-SH 38049 is a moderately worn isolated right M^2. The crown shows a square to hexagonal surface in occlusal view. The protocone is more worn than the paracone. The metacone and hypocone are as deeply worn as each other. The enamel is thick but less wrinkled than in KNM-SH 12418 which was collected previously and described as an M^2 of *Nyanzachoerus* sp. by Nakaya *et al.* (1984). The tooth has at least 5 roots, 4 large ones positioned below the main cusps and a small one below the anterior accessory cusp.

KNM-SH 40131 is a left mandibular body with P_{1-4}. P_1 and P_2 have triangular profiles in buccal and lingual views. P_1 is slightly worn, small and is directly situated anterior to of P_2 without a diastema. The protoconid is high and is positioned slightly behind the middle of the tooth. The anterior and posterior accessory cuspids are not developed. P_2 is slightly worn and is larger than P_1. The protoconid is higher and more developed than that of P_1. The anterior and posterior accessory cuspids are slightly developed. P_3 is large and moderately worn especially at the apex of the protoconid. The anterior and posterior accessory cuspids are well developed. The posterior cuspid has a cingulum-like small cuspid in the buccal side. P_4 is lower and shorter than P_3 but as wide as it. There is a small diastema between P_3 and P_4 (ca. 6 mm). The protoconid and posterior accessory cuspid are moderately worn. The anterior accessory cuspid is higher and more developed than that of P_3. The metaconid (= innenhugel) is positioned on the lingual and posterior side of the protoconid and connects to the protoconid because of moderate wear. The talonid is well developed. The posterior cingulum is strongly wrinkled and forms small cuspid-like swellings. The anterior and posterior cristids are shorter than those of P_3.

KNM-SH 40129A-D are left and right mandible bodies with left lower C, P_3, M_{1-3} and

right M_{1-3}. The mandibular body is relatively massive. The buccal wall of the body swells near M_3. The canine root is surrounded by the mandibular body and shows only the cross section. The cross section is triangular surrounded by thin enamel walls lingually and ventrally. The canine crown seems to be situated near the P_1 and there is probably no long diastema between the lower canine and P_1. The crown and roots of P_1 are not available but are thought to be present directly in front of P_2 without a long diastema. The crown of P_2 is also broken away but the two roots are preserved in the mandibular body. P_3 is large and triangular in lateral view. The protoconid is high. Only the posterior side of the protocone is worn. The anterior accessory cuspid is not developed. The posterior accessory cuspid is developed. P_4 is missing but estimation of the P_4 length is possible. M_1 is much smaller than P_3 and well worn. The enamel is thick and heavilly wrinkled. The anterior accessory cuspid and anterior cingulum are lightly developed. The posterior accessory cuspid and posterior cingulum are well developed. M_2 is larger and more worn than M_1. The enamel is thicker and more wrinkled. The posterior accessory cuspid and posterior cingulum are also more developed than those of M_1. M_3 is slightly worn. The enamel is less wrinkled than in KNM-SH 14758. The talonid is not well developed, and the length and width are short. The cuspids are moderately columnar. The talonid is positioned laterally, just behind the entoconid and has one developed cuspid. The position of the talonid is probably caused by the small mandibular body which does not have enough space for a large M_3, the M_3 in this specimen is of the small type.

KNM-SH 38050 is a posterior right M_1 fragment. It is not worn. The enamel is thin and heavily wrinkled. The posterior cingulum is well developed.

KNM-SH 38048 is a posterior right M_2 fragment. It is not worn. The enamel is thin and deeply wrinkled. The posterior accessory cuspid is well developed and almost half the size of the metaconid and hypoconid. The 2/3 cusplet is also developed and one third of the size of the metaconid and hypoconid. The posterior cingulum and basal pillar are slightly developed.

KNM-SH 38051 is a right mandibular fragment with M_3 which was still erupting up at the time of death, and roots of P_4-M_2. The width of M_3 is estimated to be 19 mm and the length is not available but apparently less than 35 mm. The size of the M_3 indicates that it could belong to *N. devauxi*. The enamel is moderately wrinkled. The anterior accessory cuspid and anterior cingulum is well developed. The talonid is not available. The cross sections of the tooth roots are available. P_4 has 3 roots. The anterior one is large and well curved. The posterior two are fused to each other. M_1 and M_2 have 4 roots respectively the cross sections of which are circular to ovate. Measurements of the tooth are given in Table 11.

The small Namurungule *Nyanzachoerus* is characterized by the presence of P_1, absence of diastema between P_{1-2} and short and narrow M_3 with weakly developed talonid.

In the Namurungule Formation, P_1 is available only in KNM-SH 40131. In the other localities, P_1 in the small and primitive species of *Nyanzachoerus* is poorly represented. P_1 is present in *N. devauxi* and *N. syrticus* of the Sahabi Formation, Libya and in *N. tulotos* of the Lothagam 1 Formation, Kenya (Cooke, 1987; Cooke & Ewer, 1972; Leonardi, 1952, 1954). The other large and advanced species of *Nyanzachoerus* lack P_1 (Cooke & Wilkinson, 1978). Measurements of P_1 of *Nyanzachoerus* species are given in Table 12. The length of P_1 of KNM-SH 40131 is greater than in any other specimens. The breadth is narrow, similar to that of *N. devauxi* from the Sahabi Formation. There is no diastema

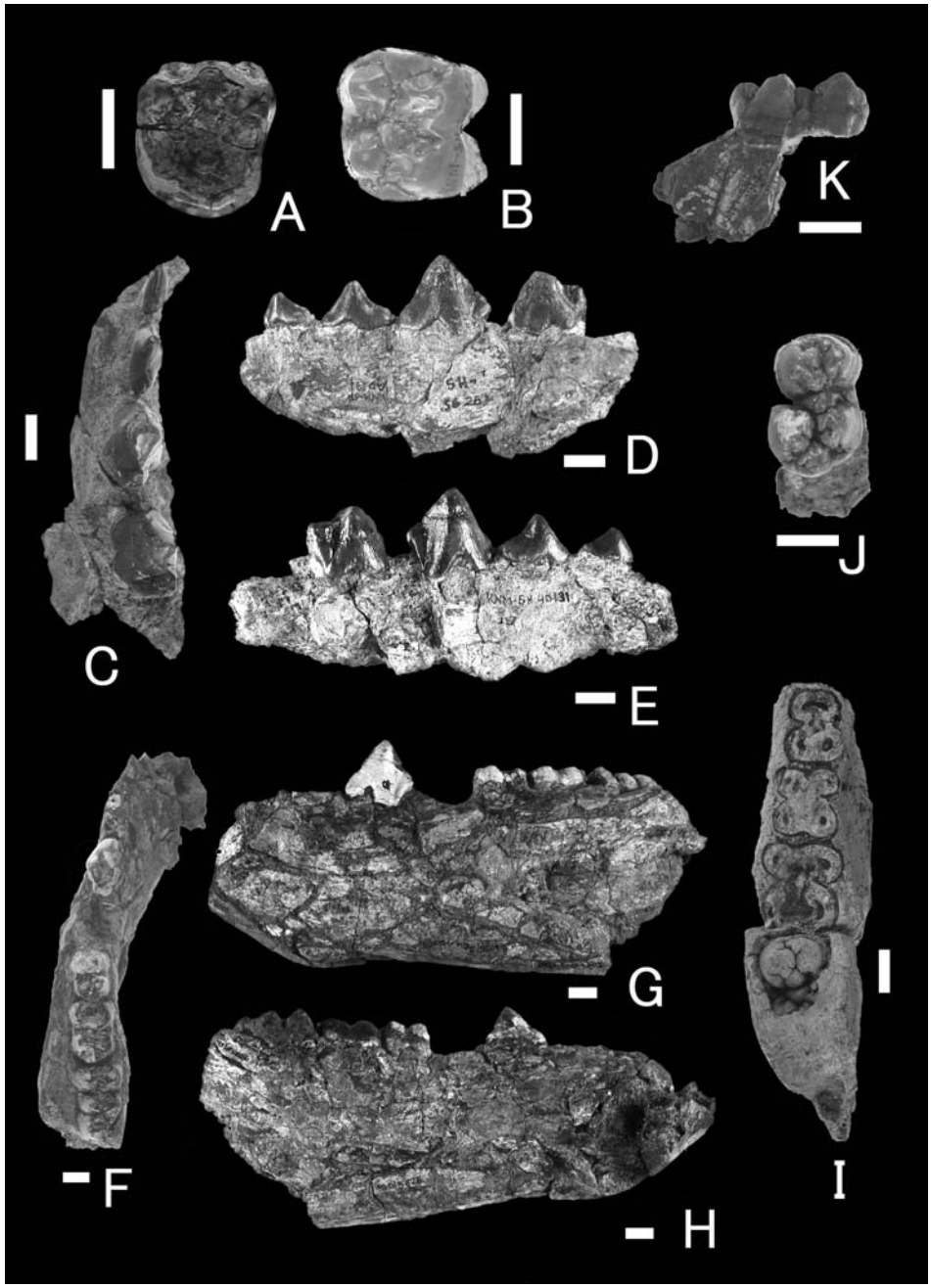

Fig. 7. A-K: *Nyanzachoerus* cf. *devauxi*. A) occlusal view of the right P^4 (KNM-SH 18002); B) occlusal view of the right M^2 (KNM-SH 38049); C) occlusal, D) buccal and E) lingual views of the left mandible with P_{1-4} (KNM-SH 40131); F) occlusal, G) buccal and H) lingual views of the left mandible with P_2-M_3 (KNM-SH 40129A); I) occlusal view of the right mandible with P_4-M_3 (KNM-SH 38051); J) occlusal and K) buccal views of the right M_2 (KNM-SH 40152). Scales in cm.

Table 11. Measurements (mm) of the teeth of *Nyanzachoerus* cf. *devauxi*.

Material	Part	Length	Breadth	Height
SH 38417	I^2	18.2	9.8	8.5
SH 18002	P^4	17.7	21.6	-
SH 38049	M^2	22.6	21.1	-
SH 41908	M^1	c. 19	17.3	c.9
SH 41909	I_2	14.9	8.3	-
SH 40131	P_1	13.7	5.7	9.2
SH 40129A	P_2	17.1	-	-
SH 40131	P_2	19.2	8.2	12.8
SH 40129A	P_3	23.7	14.8	24.2
SH 40131	P_3	23.2	15.5	22.3
SH 40142	P_3	27.7	16.0	18.4
SH 40131	P_4	19.5	15.4	18.0
SH 40142	P_4	23.3	14.5	12.4
SH 40129A	M_1	19.3	14.5	9.4
SH 40129C	M_1	19.5	14.6	9.6
SH 40129A	M_2	23.4	17.6	8.6
SH 40129B	M_2	23.0	17.2	8.1
SH 40152	M_2	25.2	18.3	13.5
SH 40129A	M_3	29.9	20.6	14.4

between P_{1-2} in the Namurungule specimens (e.g. KNM-SH 40131, 40129A). However, the diastema between P_{1-2} of *N. tulotos* from the Lothagam 1 Formation is very long (Cooke & Wilkinson, 1972). The diastema between P_{1-2} of *N. devauxi* from the Sahabi Formation is short (9.5 mm) (Cooke, 1987).

Two specimens of M_3 from the Namurungule Formation are available, KNM-SH 40131 and 14760 (Nakaya *et al.*, 1987). Measurements of M_3 of small *Nyanzachoerus* species are given in Table 13. M_3 is short and narrow in the Namurungule specimen and *N. devauxi*. However, it is long and narrow in *N. waylandi* and long and wide in *N. syrticus* and *N. tulotos*.

These characters indicate that the Namurungule suid is most likely to be *N. devauxi*. The other species of *Nyanzachoerus* are much larger, for example, the length of M_3 is more than 50 mm.

? *Nyanzachoerus devauxi* (Arambourg, 1968)
(Figs. 8E-F)

Material: Left lower premolar (KNM-SH 18010, locality unknown)
Horizon: Unknown Member of the Namurungule Formation

Description

KNM-SH 18010 is an isolated lower premolar with two roots. It is similar to P_1 of *Nyanzachoerus devauxi* (KNM-SH 40131) in length and breadth. Measurements of the tooth are 13.9 mm in length, 5.4 mm in breadth and 11.0 mm in height. However, there are several differences between them. The protoconid is positioned in the middle of the crown in KNM-SH 18010 whereas it is positioned anteriorly in P_1 and in the middle in P_2 of KNM-SH 40131. However, P_2 of KNM-SH 40131 (19.2 x 8.2 mm) is much larger than KNM-SH 18010. The anterior accessory cuspid is more developed than that of

Table 12. Measurements (mm) of P_1 of small *Nyanzachoerus* species (Cooke, 1987; Cooke & Ewer, 1972; Leonardi, 1952, 1954).

		Length			Breadth		
Taxon	N	min	max	ave	min	max	ave
SH 40131	1	13.7	13.7	13.7	5.7	5.7	5.7
N. devauxi	2	10.1	11.0	10.6	5.2	5.3	5.3
N. syrticus	1	11.1	11.1	11.1	7.1	7.1	7.1
N. tulotos	3	10.1	11.0	10.5	6.0	6.5	6.3

Table 13. Measurements (mm) of M_3 of small *Nyanzachoerus* species (Arambourg, 1968; Cooke, 1987; Cooke & Ewer, 1972; Pickford, 1987, 1989, 1994).

		Length			Breadth		
Taxon	N	min	max	ave	min	max	ave
SH	2	29.9	35.0	32.5	20.3	20.6	20.5
N. devauxi	4	32.0	38.0	35.0	18.3	21.0	20.1
N. syrticus	3	42.6	43.9	43.4	25.1	29.0	26.5
N. tulotos	11	36.7	48.8	42.4	21.9	24.5	23.3
N. waylandi	5	40.0	46.9	43.8	18.3	21.5	19.8

KNM-SH 40131. The posterior accessory cuspid is narrower and higher. The cristid from the protoconid to the posterior accessory cuspid is indented whereas it is flat in KNM-SH 40131. Such cristids are seen in the lower premolars of *Propotamochoerus* sp. from Pakistan. However, there are so few specimens that it is difficult to discuss the variations of the cristid.

Nyanzachoerus sp. large
(Figs. 8A-D)

Material: Left M^2 (KNM-SH 17992, locality unknown), Left $dP^{4?}$ (KNM-SH 18003, locality unknown)
Horizon: Unknown Member of the Namurungule Formation

Description

Two upper cheek teeth, KNM-SH 17992 and 18003 seem to be too large to assign to *N. devauxi*.

KNM-SH 17992 is an isolated left M^2. It is slightly worn and the anterior cusps are more worn than the posterior ones. The anterior and posterior accessory cusps are well developed. Thus the occlusal surface is hexagonal rather than square while M^2 of *N. devauxi*, KNM-SH 12418 (Nakaya *et al*., 1984) and 38049 (see above) is nearly square. The enamel is fairy thick and wrinkled. A basal pillar is present at the lingual side. The tooth is larger than M^2 of *N. devauxi*, KNM-SH 12418 and 38049. The roots are also large and small ones are present below the anterior and posterior accessory cusps. Measurements of the M^2 are 28.8 mm in length and 27.2 mm in breadth.

KNM-SH 18003 is a left upper cheek tooth crown which is as large as KNM-SH 17992. But it has strange characters for an M^2. The enamel is less wrinkled than KNM-SH 17992. The crown lacks a posterior accessory cusp and posterior cingulum. The anterior cingulum is weak. The specimen may not be *Kenyapotamus* because of the presence of the median accessory cusp. It could be an upper deciduous molar crown,

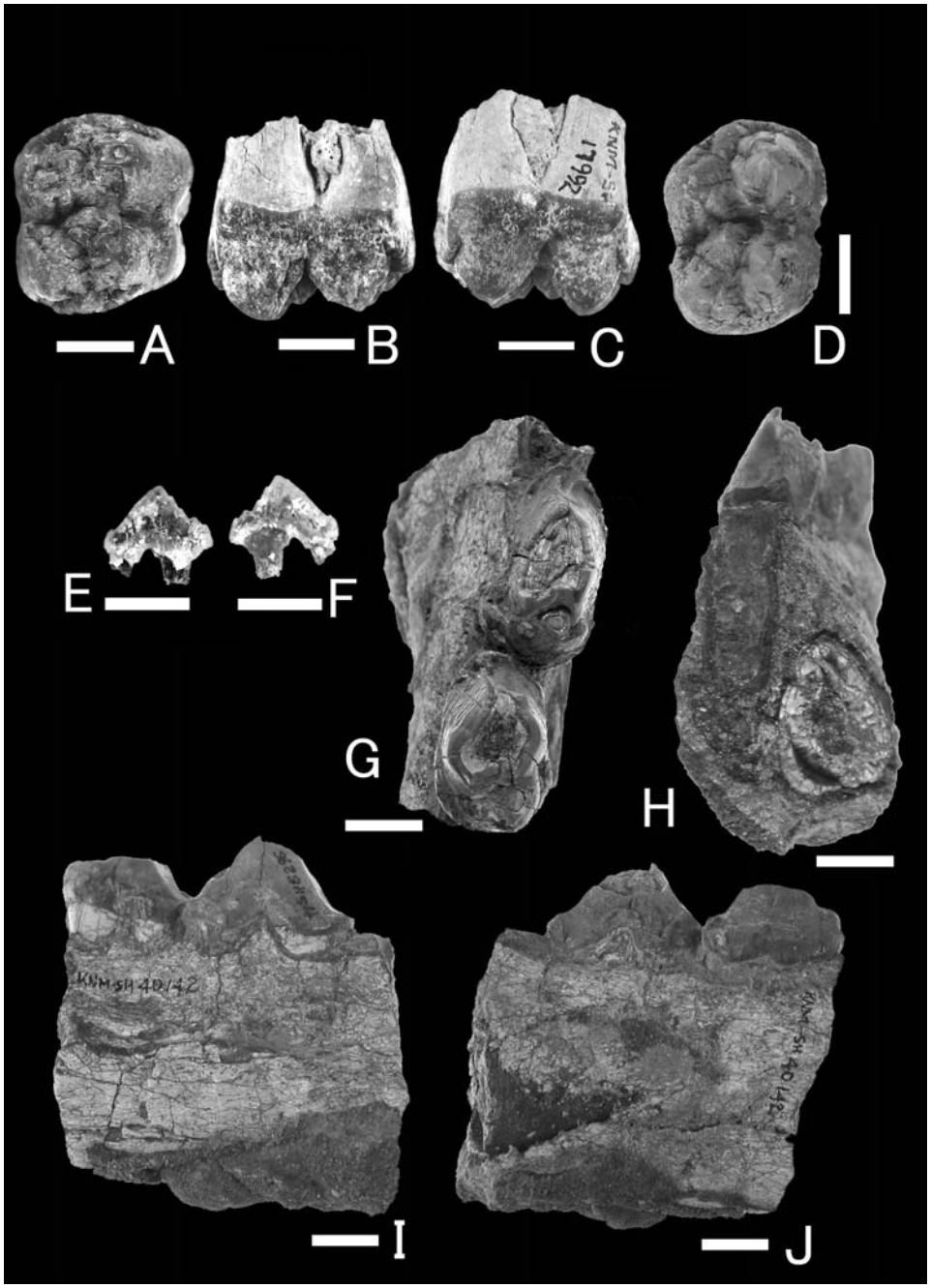

Fig. 8. A-D: *Nyanzachoerus* sp. A) occlusal, B) buccal and C) lingual views of the left M^2 (KNM-SH 17992); D) occlusal view of the left $dP^{4?}$ (KNM-SH 18003). **E-F:** ? *Nyanzachoerus devauxi*. E) buccal and F) lingual views of the left lower premolar (KNM-SH 18010). **G-J:** *Kenyapotamus coryndoni*. G) occlusal, H) anterior, I) buccal and J) lingual views of the right mandible with P_{3-4} (KNM-SH 40142). Scales in cm.

probably dP^4. Measurements of the teeth are 29.8 mm in length and at least 23.5 mm in breadth.

The identification of these two specimens is difficult. The size and shape of M^2 and dP^4 are variable in the same species (e.g. Pickford, 1989, 1990). The most primitive and oldest known *Nyanzachoerus* is *N. devauxi* and the second oldest is *N. syrticus* which is larger than *N. devauxi*. These two specimens from the Namurungule Formation are most likely to belong to one or other of these species. Their measurements do not exclude this possibility. However, it is possible that these specimens belong to large individuals of *N. devauxi*.

Family Hippopotamidae Gray, 1821
Genus *Kenyapotamus* Pickford, 1983
Kenyapotamus coryndoni Pickford, 1983
(Figs. 8G-J)

Material: Right upper molar fragment (KNM-SH 18001, loc. SH 22), right M^2 (KNM-SH 41516, loc. SH 81), right mandible with P_{3-4} (KNM-SH 40142, loc. SH 81)
Horizon: The Lower Member of the Namurungule Formation

Description

Previously, a well-preserved mandible of an old individual, several teeth and postcranial bones were collected during the 1982 and 1984 field seasons (Nakaya, 1994; Nakaya *et al.*, 1984, 1987) . However, only tooth and mandibular fragments were added during the 1986 and 1999 field seasons.

KNM-SH 18001 is a right upper molar fragment preserving posterior columns, metacone, hypocone, talon and posterior cingulum. It is little or not worn. The cusps are conical and the posterior cingulum is high and well developed. The furchen are deep. The posterior accessory cusp connects to the hypocone. The tooth is slightly larger than KNM-SH 15850 and 15851 (Nakaya *et al.*, 1987), but as large as the upper first molar of the Ngerngerwa Formation (KNM-BN 1494).

KNM-SH 40142 is a right mandible fragment with P_{3-4} also including a canine root. The canine root extends at least below the end of P_3. The cross section is ovate triangular. P_3 being well worn lacks the tip of the protoconid. The cingula are well developed anteriorly, buccally and lingually. The posterior accessory cuspids are well developed. The cristid between protoconid and paraconid makes a strong ridge. Measuments of the P_3 are 27.7 mm in length, 16.0 mm in breadth and 18.4 mm in height. P_4 is a slightly smaller tooth than P_3 and is well worn. The anterior cristid is shorter than that of P_3. The posterior accessory cuspids and cingula are weaker than those of P_3. Measuments of the P_4 are 23.3 mm in length, 14.5 mm in breadth and 12.4 mm in height.

KNM-SH 41516 is a slightly worn posterior part of a right M_2 crown.

The specimens clearly resemble other material attributed to *Kenyapotamus coryndoni* from the Namurungule Formation by Nakaya (1994) and Nakaya *et al.* (1984, 1987).

The genus *Kenyapotamus* was erected by Pickford (1983) and it comprises two species, *K. ternani* and *K. coryndoni*. The specimens of *Kenyapotamus coryndoni* from the Namurungule Formation are larger than *K. ternani* and as large as *K. coryndoni* from the Ngerngerwa and Nakali Formations.

Suborder RUMINANTIA Scopoli, 1777
Family Giraffidae Gray, 1821
Genus *Palaeotragus* Gaudry, 1861
Palaeotragus cf. *germaini* Arambourg, 1959
(Figs. 9A-M)

Material: Right P^2 (KNM-SH 37887 loc. SH 62), right P^3 (KNM-SH 37892 loc. SH 32), left M^{1-2} (KNM-SH 37888 loc. SH 69), left $M^{1 or 2}$ (KNM-SH 37898, 40145 loc. SH 9), right $M^{1 or 2}$ (KNM-SH 37894 loc. SH 76), posterior fragment of left $M^{1 or 2}$ (KNM-SH 40140 loc. SH 76), right upper molar (KNM-SH 37895 loc. SH 9), left upper molar fragment (KNM-SH 39908, 40126 loc. SH 69, 41766A loc. SH 66), upper molar fragment (KNM-SH 37908 loc. SH 69), left mandible with P_4-M_1 (KNM-SH 37900 loc. SH 9), right mandible with P_4-M_1 (KNM-SH 37891 loc. SH 37891), left mandible with M_{1-3} (KNM-SH 37905 loc. SH 66), left P_3 (KNM-SH 37896 loc. SH 22), right P_3 (KNM-SH 18005 loc. SH 22, 37901 loc. SH 22), right P_4 (KNM-SH 41766C loc. SH 66), left M_3 (KNM-SH 37893 loc. SH 9), left lower molar (KNM-SH 39911 loc. SH 69)
Horizon: The Lower and Upper Members of the Namurungule Formation

Description

Numerous giraffid teeth and several mandible fragments were collected during the 1986, 1998 and 1999 field seasons.

KNM-SH 37887 is an isolated premolar fragment being probably P^2 because the metacone is positioned anteriorly. The crown preserves the buccal side but the lingual part is broken; it possesses at least three roots, antero-buccal, postero-buccal, and mid-lingual ones; it is moderately worn. The paracone is well restricted, is pointed buccally and is slightly curved posteriorly from the anterior margin of the tooth. The metacone is high, pointed antero-buccally and approaches the paracone. The metastyle is not restricted, but is pointed posteriorly. The cristae are well wrinkled and the ectoloph is 'W' shaped as in *Palaeotragus primaevus* from Fort Ternan (Churcher, 1970). The main fossette is well wrinkled. Behind the protocone, a medial accessory crista is branched and makes a small accessory fossette in the postero-lingual side of the main fossette. The antero-posterior length is larger than *P. primaevus* but smaller than *P. germaini* from the type locality (Arambourg, 1959).

KNM-SH 37892 is an isolated right P^3. The tooth has three roots which are situated in antero-buccal, postero-buccal and mid-lingual sides. The occlusal surface is triangular to subcircular with rounded corners. The protocone is moderately pointed lingually and is positioned in the middle of the occlusal surface. The paracone is pointed postero-buccally and positioned posteriorly from the anterior margin of the crown. The metacone is pointed antero-buccally and approaches the paracone. The metastyle is weakly pointed posteriorly. The fossette is closed by the wrinkled enamel. The protocone and metaconule are separated by the branch of the fossette. A small accessory fossette is present in the metaconule region. The antero-posterior length is greater than in KNM-SH 37887.

KNM-SH 40145 is a well worn left upper molar in a maxilla fragment. The parastyle, paracone, mesostyle and metastyle are well pointed buccally. The metacone is weakly pointed buccally. The paracone does not connect to the mesostyle but only attaches. The protocone is restricted. The anterior cingulum is low but long, extending to the level of

the medial margin of the paraconid. An ectostyle is present between the protocone and metaconule. It is antero-posteriorly elongated and rugose like a small cingulum. A short lingual cingulum is present behind the entostyle. The folding is only present in the posterior region of the metaconule and is very small. The buccal cingula are present. The anterior one around the paracone is strong. The posterior one around the metacone is fairly small.

KNM-SH 37894 is a right $M^{1 \text{ or } 2}$ fragment the buccal side of which is broken. It is well worn. The enamel wrinkling is simple. Only the posterior side of the pli-post fossette has a small branch pointing anteriorly. The posterior side of the pli prefossette does not branch but is developed. A weak and small lingual cingulum runs around the protocone and metaconule. The entostyle was probably present but is broken.

KNM-SH 37888 are broken left upper M^{1-2} fragments. Both teeth preserve only buccal parts without the lingual ones. These teeth are fairly worn and weathered in the occlusal surface. In M^1, the parastyle, paracone and mesostyle are well pointed. The paracone is broken. The metacone is not pointed. The metastyle is weakly pointed posteriorly. The anterior part of the buccal wall is rugose but the posterior one is less rugose. The lingual cingulum is moderately developed. The paraloph and metaloph are 'W' shaped. M^2 has almost the same characters as M^1. However, it preserves the buccal parts of the pli-prefossette, the anterior part of the metaconule loph and pli-postfossette the tips of which are not branched but slightly developed. The antero-posterior lengths are only available in KNM-SH 37888. These lengths are much larger than *P. primaevus* but slightly smaller than *P. germaini*.

KNM-SH 37895 is a well worn isolated right upper $M^{1 \text{ or } 2}$ crown. The posterior part of the crown is broken. The parastyle, paracone and mesostyle are pointed buccally. The buccal cingulum is present from the parastyle to mesostyle. The anterior cingulum is present in front of the protocone. The entostyle is present between the protocone and metaconule. The small lingual cingulum runs in front of the entostyle and behind the protocone. The enamel wrinkling is simple. There is no branch in the fossettes.

KNM-SH 37898 is a well worn left upper $M^{1 \text{ or } 2}$ fragment lacking the parastyle, metastyle and lingual part of the tooth. The enamel is moderately wrinkled. The anterior part of the metacone branches. However, the posterior parts of the protocone and metacone do not branch. The paracone and mesostyle are well pointed buccally. The paracone and metacone connect together at the mesostyle.

KNM-SH 39908 is a well worn posterior fragment of $M^{1 \text{ or } 2}$. The metaconule has a little folding in the posterior region.

KNM-SH 40140 is a slightly worn M^1 fragment preserving the posterior part of the crown and a partial protocone. The enamel folding pattern is simple. It has no folding in the protocone and metaconule.

KNM-SH 18005 is an isolated right P_3. The tooth is slightly worn at the top of the cristids and is trapezoidal the lingual line of which is longer than the buccal one in occlusal view. The parastylid is separated from the paraconid and is pointed antero-lingually. The cristid of the paraconid runs bucco-lingually. The protoconid is most developed and highest in the P_3 cuspids. The metaconid is positioned postero-lingually from the protoconid, the cristid of which approaches the entoconid but does not connect to it. The cristids of the entoconid and entoconulid run postero-lingually in parallel and connect together distally.

Table 14. Measurements (mm) of the teeth of *Palaeotragus* cf. *germaini*.

Specimen	Part	Length	Mesial width	Midwidth	Distal width	Height
SH 37892	P^3	25.3	16.1	22.8	17.6	14.5
SH 37887	P^2	21.1	-	-	-	16.7
SH 37888	M^1	28.1	-	-	-	14.4
SH 37894	$M^{1 \text{ or } 2}$	23.7+	-	-	-	-
SH 37895	$M^{1 \text{ or } 2}$	28.3	-	-	-	9.5
SH 40140	$M^{1 \text{ or } 2}$	-	-	-	25.3	20.6
SH 40145	M^2	30.6	30.3	-	27.2	16.6
SH 37888	M^2	27.8+	-	-	-	15.3
SH 37898	M^2	-	-	-	-	12.0
SH 40126	M^3	-	-	-	-	-
SH 37908	M^x	-	-	-	-	-
SH 41766A	M^x	-	-	-	-	-
SH 18004	P_2	17.7	6.6	8.4	7.7	15.4
SH 18005	P_3	25.0	10.3	13.3	13.6	15.0
SH 37896	P_3	23.6	8.0	12.9	15.9	15.2
SH 37901	P_3	22.3	9.8	10.9	13.2	15.8
SH 37891	P_4	26.3	13.5	16.4	16.4	17.7
SH 37900	P_4	24.4	12.1	14.4	14.5	12.5
SH 41766C	P_4	25.8	12.2	15.9	16.4	13.1
SH 37891	M_1	27.3	18.5	-	19.1	15.5
SH 37900	M_1	23.3	15.4	-	16.1	10.3
SH 37905	M_1	24.5+	16.3+	-	17.8+	-
SH 37893	M_3	37.5	17.3	16.1	10.9	18.2
SH 37905	M_3	ca.38.8	-	16.7	-	10.7
SH 37911	M_x	30.6+	19.6+	-	-	ca.20
SH 37888	M^{1-2}	ca.55 (total length)				
SH 37891	P_4-M_1	56.2 (total length)				
SH 37900	P_4-M_1	47.3 (total length)				
SH 37905	M_{1-3}	91.6 (total length)				

KNM-SH 37896 is a slight worn isolated left P_3. The occlusal surface is trapezoidal. The parastylid is separated from the paraconid. The parastylid is more developed than the paraconid. The protoconid is high. The metaconid is developed and does not approach the entoconid. A weak anterior cingulum is present in the antero-buccal side of the protoconid. The entoconid and entoconulid do not connect to each other because of the slight wear.

KNM-SH 37891 is a right mandible fragment with P_4-M_1. The P_4 is only slightly worn and molarized. Because of the light wear, the protoconid does not connect to the parastylid and paraconid. The protolophid branches in the posterior region. The buccal branch approaches the hypoconid and the lingual one the entoconid. However, the two do not connect but are only directed towards each other. The paraconid does not connect because of the slight wear. The hypoconulid loph has a small branch directed towards the entoconid. The M_1 is more worn than the P_4. A low ectostylid (basal pillar) is present between the protoconid and hypoconid. The protolophid and paralophid connect together in the anterior region. A rugose anterior cingulum is present in the anterior region of the protoconid.

KNM-SH 37900 is a right mandible fragment with well worn P_4-M_1. The P_4 is molarized, the second lobe being one third of the antero-posterior length. The protoconid branches posteriorly, connects to the paraconid and attaches to the hypoconid.

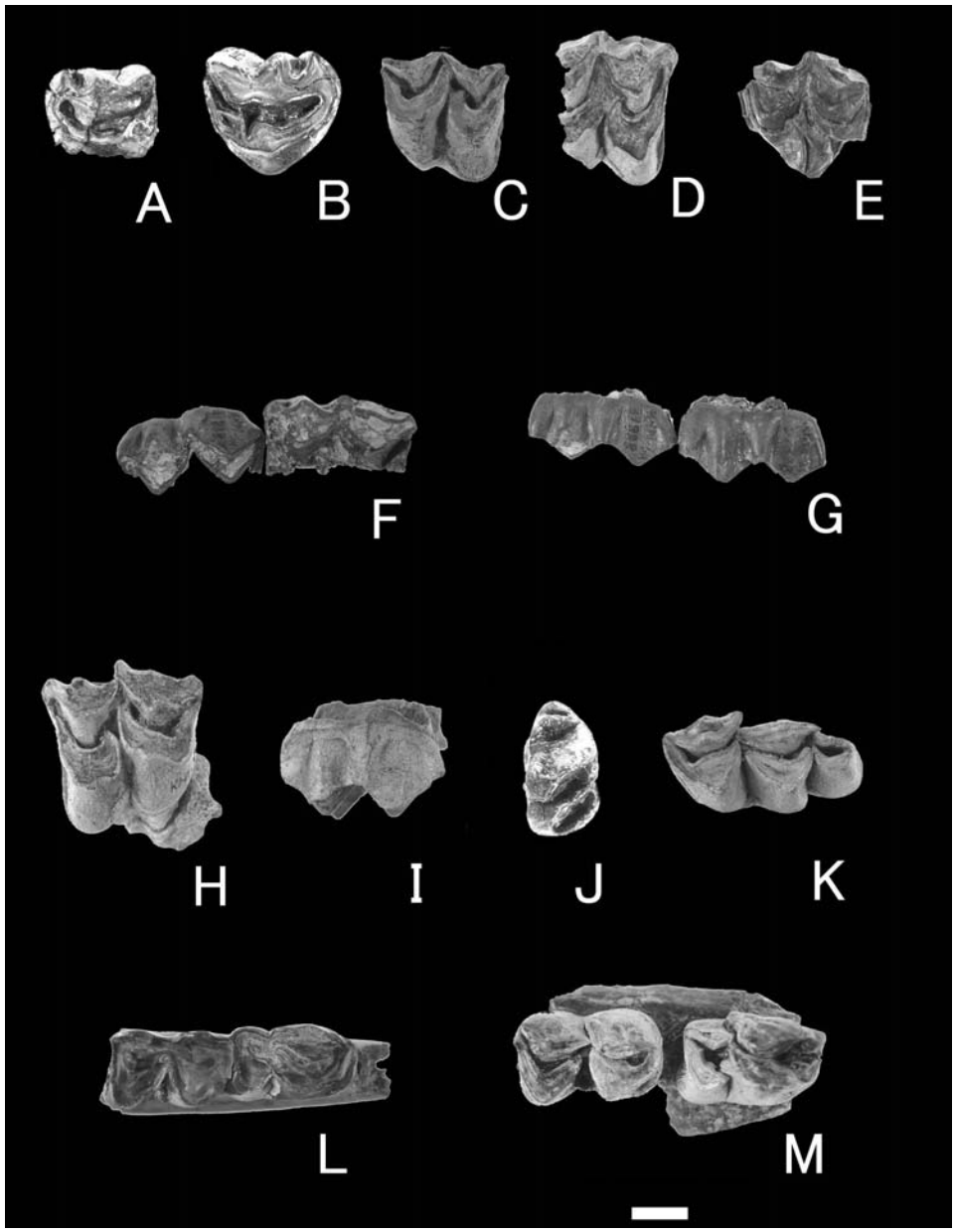

Fig. 9. A-M: *Palaeotragus* cf. *germaini*. A) occlusal view of the right P^2 (KNM-SH 37887); B) occlusal view of the right P^3 (KNM-SH 37892); C) occlusal view of the right $M^{1 \text{ or } 2}$(KNM-SH 37894); D) occlusal view of the right upper molar (KNM-SH 37895); E) occlusal view of the left $M^{1 \text{ or } 2}$ (KNM-SH 37898); F) occlusal and G) buccal views of the left M^{1-2} (KNM-SH 37888); H) occlusal and I) buccal view of the left $M^{1 \text{ or } 2}$ (KNM-SH 40145); J) occlusal view of the right P_3 (KNM-SH 18005); K) occlusal view of the left M_3 (KNM-SH 37893); L) occlusal view of the left mandible with P_4-M_1 (KNM-SH 37900); M) occlusal view of the right mandible with P_4-M_1 (KNM-SH 37891). Scale in cm.

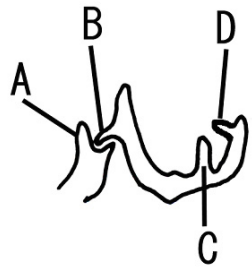

Fig. 10. Enamel plication patterns in the protocone and hypocone of giraffid upper molars (after Nakaya *et al.*, 1987). A: posterior plication of the protocone; B: anterior plication of the hypocone; C: middle plication of the hypocone; D: posterior plication of the hypocone.

Table 15. Percentages (%) of the enamel plication patterns in upper cheek teeth of the giraffid.

	N	A			B			C			D		
Taxon		2	1	0	2	1	0	2	1	0	2	1	0
P. primaevus (FT)	29	88.5	11.5	0	32.0	36.0	32.0	66.7	0	33.3	70.4	22.2	7.4
P. primaevus (BN)	14	46.1	23.1	30.8	16.7	8.3	75.0	38.5	0	61.5	69.2	30.8	0
P. cf. *germaini* (SH)	7	28.6	14.3	57.1	42.9	0	57.1	16.7	0	83.3	20.0	40.0	40.0
P. germaini (LT)	1	0	0	100	0	0	100	0	100	0	100	0	0
Samotherium (NA)	1	0	0	100	0	0	100	0	0	100	0	0	100

Loc.=locality; N = numbers of the specimens including dP^4 and M^{1-3}; Characters A-D are given in Fig. 5; 2-0 in the second line indicate the strength of enamel plication, 0: absent, 1: weak, 2: strong; FT=the Fort Ternan Foramtion; BN=the A-E Members of the Ngorora Formation; SH=the Namurungule Formation, Samburu Hills; LT=the Lothagam 1 Formation; NA=the Nakali Formation, Kenya.

Table 16. Measurements (mm) of the upper molars of African *Palaeotragus* species (Arambourg, 1959; Churcher, 1970, 1978; Hamilton, 1978).

Taxon	Part	N	Length			Breadth		
(Locality)			min	max	ave	min	max	ave
P. germaini	M^1	1	28.5	28.5	28.5	28.9	28.9	28.9
(Samburu Hills)	M^2	2	30.5	32.9	31.7	30.2	30.9	31.6
P. primaevus	M^1	13	18.6	25.0	21.5	19.9	23.2	21.1
(Fort Ternan)	M^2	6	22.0	28.0	24.6	22.7	25.5	24.4
P. primaevus(Ngorora)	M^x	3	23.0	24.0	23.3	24.0	25.0	24.7
P. germaini(Lothagam)	M^x	1	31.5	31.5	31.5	30.3	30.3	30.3
P. germaini	M^1	3	29.0	33.7	31.6	27.5	32.0	31.2
(Oued el Hammam)	M^2	3	32.3	36.0	34.1	30.0	34.2	30.3

The ectostylid is present between the protoconid and hypoconid. In M_1, the ectosylid is present between the protoconid and hypoconid. The small cingulum runs behind the ectostylid and around the antero-buccal region of the hypoconulid.

KNM-SH 37897 is a right mandible fragment with well worn M_2. This specimen comes from the same individual as KNM-SH 37900. The anterior part of the tooth is broken. A small ectostylid is present between the protoconid and hypoconid. The hypoconid and metaconid connect each other at the entoconid. The protoconid and hypoconid do not connect but only attach to each other. The protoconid connects to the metaconid. A weak posterior cingulum is present behind the hypoconid.

KNM-SH 37893 is a moderately worn isolated left lower M_3 crown. The third lobe is

not rounded but elongated antero-posteriorly and is well developed, the antero-posterior length is more than half of that of the second lobe. The protoconid is slightly restricted. The hypoconid is weakly restricted. The protoconid loph does not connect but just attaches to the parastylid. Thus, the prefossettid is closed anteriorly but open posteriorly. The midfossetid is open anteriorly and posteriorly. The postfossettid is completely closed by the hypoconulid and entoconulid. The weak and short anterior cingulum is present only in the antero-buccal region of the protoconid. A small and low ectostylid is presented between the protoconid and hypoconid. The very weak postectostylid is presented between the hypoconid and hypoconulid.

KNM-SH 39911 is an unworn left lower molar fragment which is slightly compressed bucco-lingually. The protoconid connects to the paraconid at the parastyle and branches posteriorly.

Measurements of the teeth are given in Table 14.

The Late Miocene giraffid genera present in North and Sub-Saharan Africa are *Palaeotragus*, *Samotherium* and *Giraffa*. *P. primaevus* is a small giraffid of the Middle to Late Miocene (Churcher, 1970; Hamilton, 1978). *P. germaini* is a moderate sized giraffid of the Late Miocene (Arambourg, 1959; Churcher, 1979). *P. primaevus* is known from the Fort Ternan Formation and Members A-E of the Ngorora Formation (Cherchur, 1970; Hamilton, 1978). *P. germaini* is known in Oued el Hammam, Algeria, and Lothagam 1 Formation, Kenya. *Samotherium* and *Giraffa* are much larger than the Namurungule giraffid.

Nakaya *et al.* (1987) noticed the enamel plication patterns in the protocone and hypocone of the upper molars, KNM-SH 14759 and found that they are similar to *P. primaevus* although the specimens are close in size to *P. germaini*. Later Nakaya (1994) concluded that the Namurungule *Palaeotragus* is probably a new species. However, several upper cheek teeth were collected from the Namurungule Formation during the recent field seasons and some specimens show the simple enamel patterns unlike KNM-SH 14759. The enamel plication patterns are counted in the several Middle to Late Miocene giraffids from the various localities in East Africa as follows:-

The four places (A-D) of the enamel plication of the upper cheek teeth are explained in Fig. 10. The patterns are scored as absent (0), weak (1) and strong (2). The materials include dP^4 and M^{1-3}. The results are given in Table 15. The Middle Miocene giraffid, *P. primaevus* from the Fort Ternan Formation, Kenya shows strong enamel plications in A, C and D within most of the specimens and a large variation in B. In the late Middle Miocene *P. primaevus* from the Ngorora Formation, the plications become slightly weaker within most of the specimens. The Late Miocene giraffid, *P. germaini* from the Lothagam 1 Formation including only one upper molar, shows no plication in A and B. *Samotherium* sp. from the Nakali Formation including only one upper molar, shows no plication in any of the parts. It seems that the enamel plication patterns become weaker or disappear in the more recent giraffids. In fact, the more recent giraffids, *Giraffa*, *Sivatherium* and *Okapia* show simple enamel patterns in the upper molars (Nakaya *et al.*, 1987). However, the specimens from the Nakali and Lothagam 1 Formations are few. The Namurungule giraffids show large variations in plication patterns. The ratios of the occurrence and pattern seem to be intermediate between the Middle and Late Miocene giraffids.

The sizes of the upper cheek teeth are also compared with *P. primaevus* and *P. germaini* from North and Sub-Saharan Africa. *Samotherium* and *Giraffa* species are much larger than *Palaeotragus*. Measurements of the upper molars of African *Palaeotragus* species

are given in Table 16. The upper molars of the Namurungule giraffid are larger than any specimens of *P. primaevus* from Fort Ternan and the Ngorora Formation but are close to those of *P. germaini* from the Lothagam 1 Formation, Kenya, and Oued el Hammam, Algeria. These upper cheek teeth from Samburu Hills are assigned to *P.* cf. *germaini* based on their size rather than on the enamel plication patterns which include large variations.

Family Bovidae Gray, 1821
Tribe Boselaphini Knottnerus-Meyer, 1907
Boselaphini sp. large (*Tragoportax* sp.)
(Fig. 11A)

Material: Calvarium with horn cores (KNM-SH 38322, loc. SH 70 excavation)
Horizon: The Lower Member of the Namurungule Formation

Description

A well preserved calvarium with horn cores was excavated *in situ* during the 1998 field season. This specimen, KNM-SH 38322, preserves left and right horn cores, braincase and tuberosities. Most of the occipitals and basicranium are broken. The posterior part of the braincase is deformed and is squashed to the left. It is a moderate sized *Tragoportax*. The left horn core is well preserved, and is about 220 mm long from the base but it lacks the tip. The right one preserves only the base for about 80 mm. The total length of the horn cores is estimated to be 300 mm. The horn core is compressed medio-laterally. The maximum width of the cross section lies in the middle. The cross section of the horn core is oval to triangular near the base but it becomes triangular toward the tip and is more compressed medio-laterally. The lateral surface is round and the medial is flat. Strong anterior and posterior keels are present. These keels run onto the weak pedicels. The presence of the distal demarcation is unknown because the tips are missing. The horn core is strongly spiraled anticlockwise on the right side. The lateral and medial surfaces show numerous longitudinal grooves for blood vessels near the base, but are almost smooth near the tip. There is no trace of transverse ridges. The horn core is inserted uprightly above the orbit in lateral view but curves backwards about midway. The frontals between the horn cores are flat without transverse ridges. The orbits are broken. The temporal ridges are strong and are angled postero-medially towards the nuchal crest. The surface on the frontals and parietals is fairly weathered so any sutures are not possible to observe. The brain case roof in not inclined. The posterior region of the brain case is fairly narrow because of the temporal ridges. The occipital and basioccipital are broken. Only tuberosities are preserved but they are not prominent. Several measurements of the skull are available (measurements follow the method of Thomas (1981)). Width of the foramen magnum is about 23 mm. Width across mastoids is 97.3 mm. Maximum width of brain case is 79.8 mm. Distance between horn core bases is 43.2 mm. Frontal width is at least 130 mm. Antero-posterior diameters of horn core bases are 42 mm in the left and 41 mm in the right. Transverse diameters of horn core bases are 32 mm in the left and 31.5 mm in the right.

KNM-SH 38322 is most similar to *T. cyrenaicus* especially in lateral view being compared with the cranium, AUH 442 from the Baynunah Formation, U.A.E. (Gentry, 1999). In both specimens, the horn core curves backwardly, rises upwards near the tip,

diverges widely and has strong torsion and is spiral. However, there are several differences between them. KNM-SH 38322 is smaller. There is no transverse ridge between the horn core bases. The distance between the horn cores is greater. The tips of the horn cores do not approach each other. The maximum width of the cross section lies in the middle whereas it is in more posterior in *T. cyrenaicus*. The lateral surface of the horn core is rounded whereas it is flat in *T. cyrenaicus*. The distal demarcation of the horn core is unknown in KNM-SH 38322 whereas it is present in AUH 442 and is similar to *Tragoportax* and *Miotragocerus* species. However, previously collected horn core fragments, KNM-SH 12318 and 12325 (the 1982 collections) that have the distal demarcation of the horn core described as *Miotragocerus* sp. by Nakaya (1994) and Nakaya *et al.* (1984) may also belong to the same taxon as KNM-SH 38322. Thus, KNM-SH 38322 probably loses the distal demarcation. The type specimen of *T. cyrenaicus* from the Sahabi Formation has straighter axes of the horn cores (Lehman & Thomas, 1987; Thomas, 1979).

Boselaphini sp. small (gen. et sp. nov.)

Material: Calvarium with horn cores (KNM-SH 17911, loc. SH 22 excavation), left and right horn core fragments (KNM-SH 38326 loc. SH 73), right horn core base (KNM-SH 38330 loc. SH 23), left horn core fragment (KNM-SH 38328 loc. SH 23, 38396 loc. SH 22, 38398, 41881 loc. SH 62), horn core fragment (KNM-SH 38397 loc. SH 9)
Horizon: The Lower Member of the Namurungule Formation

Description

A well preserved calvarium with horn cores, KNM-SH 17911, will be described as the type specimen of gen. et sp. nov. together with specimens from the 1982 and 1984 field seasons (Tsujikawa *et al.*, in prep). Therefore, the specimens are briefly described here. Several horn core fragments were added during the 1998 collections.

The small boselaphine bovid is spiral-horned. Weak anterior and strong posterior keels are present in the horn cores. It is the most abundant bovid but is restricted to the Lower Member of the Namurungule Formation. The species is most similar to *Sivoreas eremita* from the Ngorora Formation rather than the Sub-Parathethys spiral-horned antelopes by presence of the anterior and posterior keels, strong torsion and median crest with surrounding depressions in the frontal plane and the shape and position of the supraorbital foramen (Thomas, 1981). However, only fragmentary remains are available from the Ngorora Formation.

cf. Boselaphini sp. small

Material: Left upper molar (KNM-SH 41903 loc. SH 78), Left M^3 (KNM-SH 37890 loc. SH 9), right mandible with M_3 (KNM-SH 40125 loc. SH 22), left M_3 fragment (KNM-SH 40125 loc. SH 22)
Horizon: The Lower Member of the Namurungule Formation

Table 17. Measurements (mm) of the teeth of Boselaphini small sp. (gen. et sp. nov.).

Specimen	Part	Length	Breadth	Height
SH 41903	M^x	ca.14	ca.17	ca.6
SH 37890	M^3	16.9	17.3	13.5
SH 38323	M_3	22.7	9.2	9.2+

Description

KNM-SH 41903 is a well worn isolated left upper molar. It lacks the buccal wall and hypocone. The protocone is constricted. The central cavities are curved and separated from each other.

KNM-SH 38323 is a right mandibular fragment with well worn M_3. The occlusal surface of the crown is broken mainly on the lingual side. The buccal wall is slightly curved around the paraconid, metaconid and entoconid. The entoconulid is slightly pointed postero-lingually. The low basal pillar is present between the protoconid and hypoconid. The central cavities are slightly curved. However, it is absent in the third lobe. The third lobe is almost half the size of the other two lobes in antero-posterior length and bucco-lingual breadth.

KNM-SH 37890 is a well worn isolated upper left molar. It shows a third molar character that the posterior lobe is much smaller than the anterior one and the occlusal surface is trapezoidal. The specimen is slightly larger than KNM-SH 41903. The central cavities connect with each other.

KNM-SH 40125 is a left M_3 preserving only the broken middle and third lobes.

Measurements of the teeth are given in Table 17.

These teeth are brachyodont and in occlusal view are similar to those of *Kipsigicerus labidotus* from the Ngorora Formation. However, they are slightly larger (Thomas, 1981). The horn cores of the small boselaphine from Samburu Hills are also slightly larger than those of *K. labidotus*. Thus, these specimens are boselaphine cheek teeth and are likely to belong to the small boselaphine rather than the large one. The teeth of the latter should be larger because its horn cores are also much larger. The teeth of the other bovids of the Namurungule Formation, *Gazella* and *Pachytragus* are more hypsodont.

? Boselaphini sp. large
(Fig. 11I)

Material: Right $P_{4?}$ (KNM-SH 41882 loc. SH 61)
Horizon: The Lower Member of the Namurungule Formation

Description

KNM-SH 41882 is a lower right premolar crown preserving only the lingual side. It is brachyodont and unmolarized. The protoconid is highest in lingual view. The metaconid is not developed. The paraconid is only slightly developed lingually. The entoconid and entoconulid are relatively high and run parallel to each other. The antero-posterior length only is available (at least 16.5 mm). It is much larger than the premolar of *Kipsigicerus labidotus*. Thus this premolar is more likely to belong to the large boselaphine, *Tragoportax* sp. than to the small boselaphine from the Namurungule Formation.

Table 18. Measurements (mm) of the teeth of Antilopini gen. et sp. indet. (KNM-SH 38324).

Part	Length	Breadth	Height
P^4	7.0	7.9	8.5
M^1	10.4	8.3	9.5
M^2	11.7	9.6	10.5
M^3	10.9	8.0	8.5+
M^{1-3}	32		

Tribe Antilopini Gray, 1821
Genus *Gazella* Blainville, 1816
Gazella sp.
(Fig. 11B)

Material: Left horn core base (KNM-SH 38327 loc. SH 72)
Horizon: Unknown Member of the Namurungule Formation

Description

A left horn core fragment including the base, KNM-SH 38327, was collected during the 1998 field season. The horn core is slightly weathered and preserves the upper part of the orbit, the postcornual pit and partial supraorbital foramen. The preserved length of the horn core is about 22.5 mm above the pedicel.

It is a small gazelle. The horn core is inserted above the orbit and is compressed mediolaterally. The lateral compression of the horn core is so strong that the lateral surface of the horn core is almost flat. The medial compression is weak and the medial surface is rounded. There are no keels or torsion on the surface of the horn core. The cross section is oval to D-shaped due to the lateral compression. The pedicel is undeveloped and short (12 mm above the orbit). The postcornual pit is deeply depressed in the lateral side behind the orbit and below the horn core pedicel. The frontal is thick and not high at the medial side of the horn core. The supraorbital foramen is small and is located at the antero-medial side of the horn core base. The antero-posterior diameter of the horn core base is 24.6 mm, and its transverse diameter is 18.0 mm.

Several horn core fragments of *Gazella* were collected during the 1982 and 1984 field seasons (Nakaya *et al.*, 1984, 1987). However, some of those horn cores seem to be different from *Gazella*. They are smaller than the Namurungule *Gazella* and show an uncompressed lateral surface and subcircular cross section of the horn core, a thin frontal which is high between the orbits (e.g. KNM-SH 12320, 12323 and 12324). These specimens are likely to belong to *Antidorcas* rather than to *Gazella* because of their horn core and cranial morphologies (Gentry, 1978; Tsujikawa *et al.*, in prep.). *Gazella* sp. is confirmed only in the Upper Member of the Namurungule Formation and ? *Antidorcas* sp. is confirmed in the Lower and Upper Members of the Namurungule Formation.

Antilopini gen. et sp. indet.
(Fig. 11H)

Material: Left maxilla with P^4-M^3 (KNM-SH 38324 loc. SH 32)
Horizon: The Upper Member of the Namurungule Formation

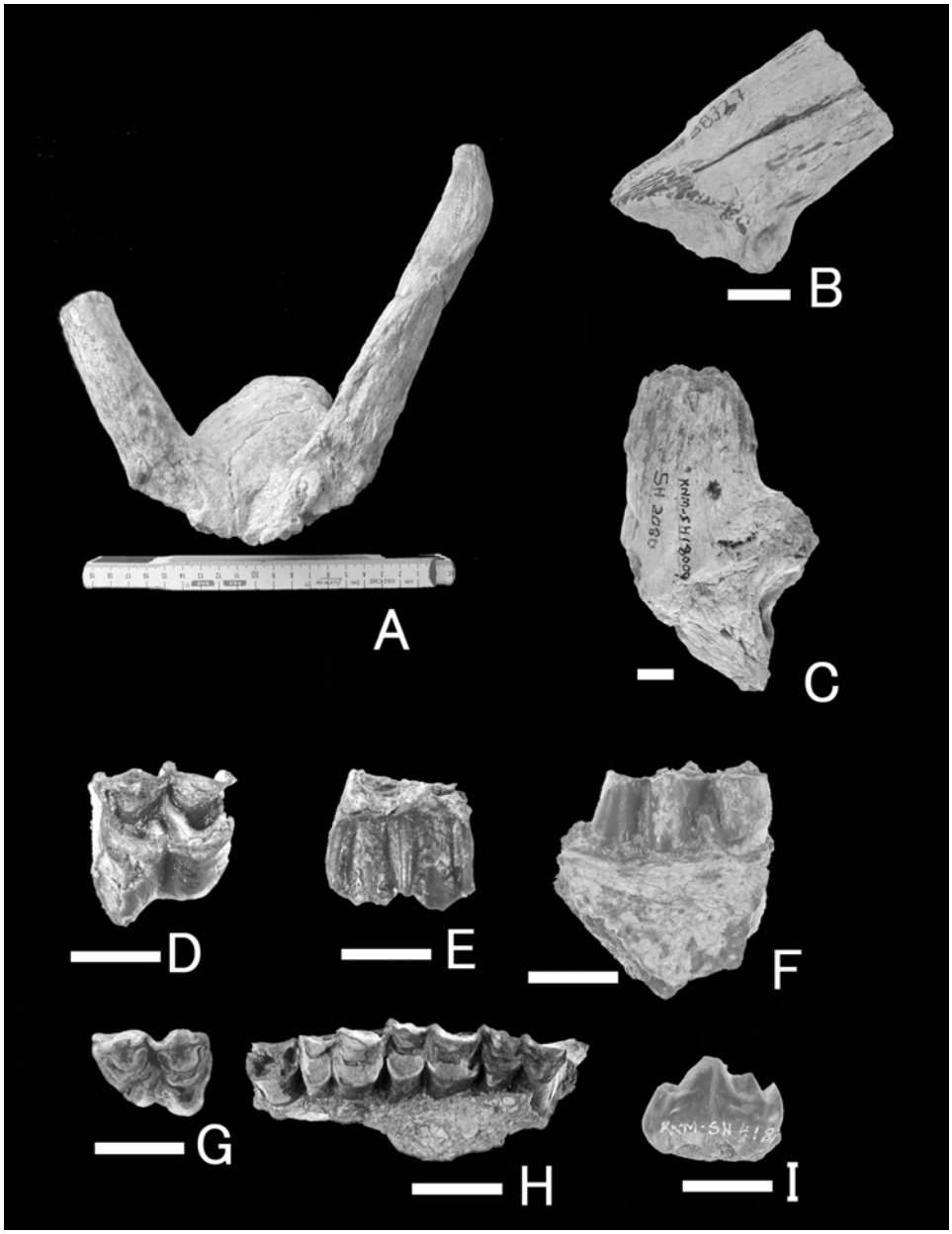

Fig. 11. A: Boselaphini sp. large. (*Tragoportax* sp.). Dorsal view of the skull (KNM-SH 38322). **B:** *Gazella* sp. Left lateral view of the horn core base (KNM-SH 38327). **C:** Bovidae gen. et sp. indet. Cranial view of the horn core base (KNM-SH 18009). **D-F:** Boselaphini small sp. D) occlusal and E) buccal views of the left M^3 (KNM-SH 37890); F) buccal view of the right M_3 (KNM-SH 38323). **G:** Reduncini gen. et sp. indet. Occlusal view of the right upper molar (KNM-SH 38329). **H:** Antilopini gen. et sp. indet. Occlusal view of the left maxilla with P^4-M^3 (KNM-SH 38324). **I:** Boselaphini sp. large. Lingual view of the right lower premolar (KNM-SH 41882). Scales in cm (B-I).

Description

A left maxilla fragment with P^4-M^3, KNM-SH 38324, was collected during the 1998 field seasons. The maxilla preserves the anterior part of the zygomatic arch. P^4, M^1 and M^2 are well worn. M^3 is almost unworn and is still erupting. Those teeth are slightly broken on the buccal side. It represents a fairly small antilopine. The buccal side of the maxilla body is flat along the tooth row. The distance between the zygomatic arch and alveolar margin is fairly short. The cheek teeth are small and moderately hypsodont. The paracone and metacone are moderately pointed and the buccal wall is relatively flat. In occlusal view, the P^4 is trapezoidal with rounded corners of the protocone. The buccal wall is almost flat but slightly depressed between the parastyle and metacone although the paracone is slightly pointed which makes a longitudinal ridge on the buccal wall. The metacone is developed. The parastyle is broken but was probably developed. There are two antero-posterior fossettes. The anterior one is relatively large, deep and placed between the protocone and paracone. The posterior one is small, shallow and placed between the protostyle and metacone. The metacone and parastyle are joined by the wall that separates the two fossettes. The protocone is not pointed or restricted on the lingual side.

On the upper molars, the paracone, parastyle and mesostyle are developed and are pointed buccally. There are no basal pillars. The central cavities are simple and slightly curved. The anterior and posterior cavities connect each other only in the unworn M^3. The protocone is not pointed lingually. The protostyle is separately pointed from the protocone posteriorly only in M^2. Measurements of the tooth are given in Table 18.

The specimen has a typical Antilopini upper dental morphology in which the cheek teeth are moderately hypsodont, the central cavities are simple in outline and are small. However, there are two Antilopini, *Gazella* sp. and ? *Antidorcas* sp. in the Namurungule Formation based on horn core and cranial morphologies (see above; Tsujikawa & Nakaya, in prep.). It is difficult to assign KNM-SH 38324 to either *Gazella* or *Antidorcas*, and it is left as Antilopini gen. et sp. indet.

Tribe Reduncini Lydekker & Blaine, 1914
gen. et sp. indet.
(Fig. 11G)

Material: Right upper molar (KNM-SH 38392 loc. SH 74)
Horizon: Unknown Member of the Namurungule Formation

Description

An isolated right upper molar, KNM-SH 38329 was collected during the 1998 field season. The tooth is small, hypsodont and well worn. There are four roots. The morphology of the occlusal surface is similar to the illustration in Gentry (1978) of the typical reduncine upper molar. The enamel surrounding the central cavities is strongly wrinkled. The buccal ribs around the paracone and metacone are strongly developed. The lingual lobe is strongly constricted around the protocone and is slightly constricted around the hypocone. The basal pillar is present and connects with the protocone.

These characters agree with the upper molars of reduncines. However, the specimen

Table 19. The updated mammal fauna from the Namurungule Formation.

Order	Family	Gen. et sp.	Member
Primates	Hominoidea	*Samburupithecus kiptalami*	L
Rodentia	Thryonomyidae	*Paraphiomys* sp.	L
		Paraulacodus sp.	L
Carnivora	Amphicyonidae or Ursidae	gen. et sp. indet.	?
	Felidae	Machairodontinae indet.	?
		Hyaenidae spp.	L, U
Proboscidea	Gomphotheriidae	*Tetralophodon* sp. nov.	L, U
		Choerolophodon sp.	L
	Deinotheriidae	*Deinotherium* sp.	L, U
Hyracoidea	Pliohyracidae	gen. et sp. indet.	L
Perissodactyla	Equidae	*Hipparion africanum*	L, U
	Rhinocerotidae	*Paradiceros mukirii*	L, U
		Chilotheridium pattersoni	L
		Kenyatherium bishopi	L
		Iranotheriinae sp. nov.	L
	Chalicotheriidae	gen. et sp. indet.	U
Artiodactyla	Suidae	*Nyanzachoerus* sp. small (*N.* cf. *devauxi*)	L, U
		Nyanzachoerus sp. large	?
	Hippopotamidae	*Kenyapotamus coryndoni*	L, U
	Giraffidae	*Palaeotragus* cf. *germaini*	L, U
		? *Samotherium* sp.	L, U
	Bovidae	Boselaphini sp. large (*Tragoportax* sp.)	L
		Boselaphini sp. small (gen. et sp. nov.)	L
		Reduncini indet.	?
		Gazella sp.	U
		Antidorcas sp.	L, U
		Pachytragus sp.	L
		Bovidae indet.	?

is the first discovery of the tribe in the Namurungule Formation and no reduncine horn cores are confirmed there. It is difficult to assign a generic name to the specimen.

Measurements of the tooth are 13.6 mm in length, 9.3 mm in breadth and 14.6 mm in height.

Bovidae gen. et sp. indet.
(Fig. 11C)

Material: Left horn core base (KNM-SH 18009 locality unknown)
Horizon: Unknown Member of the Namurungule Formation

Description

KNM-SH 18009 preserves a basal part of the horn core, a partial frontal around the orbit whose posterior parts are missing. The horn core is massive and is not compressed mediolaterally. The cross section seems to be oval or subcircular although the posterior part is missing. The horn core stands upright as in *Pachytragus*, however the pedicel is more developed. The frontal plane between the horn cores is fairly thick, thicker than the specimens of *Pachytragus* sp. from the Namurungule Formation. And it is higher than the orbital rims between the horn cores. Anterior keel and strong torsion are not evident in the horn core.

Table 20. The Late Miocene mammal localities from East Africa.

Ma	Locality
5	Adu-Asa (E)
	Manonga Valley (T)
6	Lukeino (K), Nkondo, Upper Oluka (U)
	Kanam, Mpesida (K)
7	Lower Nawata (K)
8	Lower Oluka (U)
9	
	Namurungule, Nakali (K)
10	Ngerngerwa (K)
	Kakara (U), Ngorora E (K), Ch'orora (E)

E: Ethiopia; K: Kenya; T: Tanzania; U: Uganda.

Tale 21. Mammalian faunal resemblance between the Namurungule and the other faunas during the Late Miocene in East Africa.

Locality	fam.	gen.	sp.
Ngorora A-D	68.8	33.3	10.0
Ngorora E	100.0	50.0	16.7
Ngerngerwa	77.8	66.7	40.0
Nakali	81.8	77.8	33.3
Ch'orora	88.9	60.0	0
Mpesida	72.7	20.0	0
Lukeino	75.0	16.7	0
Toluk	75.0	33.3	0

fam.: family level; gen.: generic level; sp.: specific level.

Boselaphini sp. large and sp. small, *Gazella* and *Pachytragus* are known in the Namurungule Formation (See above; Nakaya, 1994). However, KNM-SH 18009 is different from these genera in the following respects. It is larger than Boselaphini sp. small and *Gazella*. The pedicel is more prominent than in Boselaphini spp. and *Pachytragus*. The horn core does not have the anterior keel whereas it does in Boselaphini spp. The horn core is not compressed medio-laterally whereas it is compressed in *Pachytragus*.

DISCUSSION AND CONCLUSION

On the basis of the specimens collected during the 1986, 1998 and 1999 field seasons, the Namurungule fauna is updated (Table 19). Amphicyonidae/Ursidae, *Choerolophodon* sp., Pliohyracidae gen. et sp. and Reduncini gen. et sp. indet. are new discoveries. *N.* cf. *devauxi* and *P.* cf. *germaini* are revised on the basis of well preserved material. The result is that there are at least 27 species in the Namurungule mammal fauna.

Although the Latest Miocene (7.5 - 5.5 Ma) faunas are relatively well known, the early Late Miocene (10.5 - 7.5 Ma) faunas are poorly known in Sub-Saharan Africa (Table 20). However, the Namurungule Fauna is one of the best represented for this age. For example, the Nakali Fauna, Kenya, consists of 12 species (Aguirre & Leakey, 1974; Aguirre & Guérin, 1974; Pickford & Fischer, 1987), the Ch'orora Fauna, Ethiopia, consists of 12 species (Jacobs, *et al.*, 1980; Kalb *et al.*, 1982a, 1982b, 1982c; Geraads,

1997, 2001), the Ngorora upper E Fauna, Kenya, consists of 6 species (Benefit & Pickford, 1986; Pickford, 2002), the Ngerngerwa Fauna, Kenya, consists of 8 species (Benefit & Pickford, 1986; Pickford, 2002).

Mammalian faunal resemblance between the Namurungule Formation and the other localities during the late Middle and Late Miocene in East Africa is briefly examined following Nakaya (1994) because those faunas have also been updated and new faunas were added after his work. The Simpson's Index is used as a method that was explained by Nakaya (1994) and Simpson (1960). The results are given in Table 21. The Namurungule fauna indicates strong resemblance to the early Late Miocene faunas of East Africa. At the specific level, the Namurungule fauna indicates resemblance to the Ngerngerwa (40 %) and Nakali (33.3 %) faunas. At the generic level, the Namurungule fauna indicates resemblance to the Nakali (77.8 %), Ngerngerwa (66.7 %), Ch'orora (60 %) and Ngorora E (50 %) faunas. At the family level, the Namurungule fauna indicates resemblance to the Ngorora E (100 %), Ch'orora (88.9 %), Nakali (81.8 %) and Ngerngerwa (77.8 %) faunas.

However, the Namurungule fauna indicates weak resemblance to the late Middle and Latest Miocene faunas in East Africa. At the specific level, the Namurungule fauna does not indicate resemblance to the Ngorora A-D (10 %), Mpesida (0 %), Lukeino (0 %) and Tuluk (0 %) faunas. At the generic level, the Namurungule fauna indicates only weak resemblance to the Ngorora A-D (33.3 %), Toluk (33.3 %), Mpesida (20 %) and Lukeino (16.7 %) faunas. Only at the family level does the Namurungule fauna indicate strong resemblance to the Ngorora A-D (68.8 %), Mpesida (72.7 %), Lukeino (75 %) and Toluk (75 %) faunas. These results suggest great faunal changes between 10.5 Ma and 7.5 Ma. In fact, Pickford (1981) took those faunal changes and faunal resemblance as a basis for defining Faunal Sets for the biostratigraphy of East Africa.

Faunal resemblances between the Lower and Upper Members of the Namurungule Fauna also are examined. They indicate strong resemblance to each other, 81.8 % at the specific level, 88.9 % at the generic level and 100 % at the family level. Therefore, the Lower and Upper Members of the Namurungule Fauna are not different from each other.

ACKNOWLEDGEMENTS I am deeply grateful to Professor Hidemi Ishida, Drs Masato Nakatsukasa and Naomichi Ogihara of Kyoto University for continuous guidance during the course of this work. A special thanks goes to Professor Hideo Nakaya of Kagawa University and Dr Martin Pickford of Collège de France and the Muséum National d'Histoire Naturelle, Paris, who has supervised my graduate study. I am much indebted Drs Alan Gentry of British Museum (Natural History), Herbert Thomas and Brigitte Senut of the Muséum National d'Histoire Naturelle, Paris, Geneviève Bouvrain of Laboratoire de Paléontologie et Vertébrés et de Paléontologie Humaine, Université de Paris VI, Claude Guérin of l'Université de Lyon I, Yutaka Kunimatsu of Primate Reserch Institute, Kyoto University for much support and discussions. Professors Shiro Ishida of Yamaguchi University, Yoshihiro Sawada of Shimane University and Drs Katsuhiro Nakayama of Shimane University, Yoshihiko Nakano of Osaka University and Daisuke Shimizu of Roehampton University (London), Mr Joseph Mutava, Mr Wambua Mangao and Mr Onyango Blasto of the National Museums of Kenya, Mr Kiptalam Chepboi and people of Nachola are much thanked for collaboration in the field. This study is supported by a Grand-in-Aid for 21st Century COE Research Kyoto University (A14).

REFERENCES

Aguirre, E. & C. Guérin 1974. Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kenya). *Estudios Geológicos*, 30: 229-233.

Aguirre E. & P.H. Leakey 1974. Nakali: nueva fauna da *Hipparion* del Rift Valley de Kenya. *Estudios Geológicos*, 30: 219-227.

Arambourg, C. 1959. Vertébrés continentaux du Miocène supéreur de l'Afrique du Nord. *Publications du Service de la Géologique de l'Algérie (nouvelle serie), Paléontologie Memoir*, 4: 1-161.

——— 1968. Un Suidé fossile nouveau du Miocène supérieur de l'Afrique du nord. *Bulletin Société Géologique de France Paris*, (7)10: 110-115.

Benefit, B.R. & M. Pickford 1986. Miocene fossil cercopithecoids from Kenya. *American Journal of Physical Anthropology*, 69: 441-464.

Bishop, L.C. 1994. *Pigs and the Ancestors: Hominids, Suids and Environments during the Plio-Pleistocene of East Africa.* Ph.D. Dissertation, Yale University.

Bishop L.C. & A. Hill 1999. Fossil Suidae from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In (P.J. Whybrow & A. Hill, eds.) *Fossil Vertebrates of Arabia*, pp. 254-270. Yale Univ. Press, New Haven and London.

Brunet, M., F. Guy, D. Pilbeam, H.T. Mackaye, A. Likius, D. Ahounta, A. Beauvilain, C. Blondel, H. Bocherens, J.-R. Boisserie, L. de Bonis, Y. Coppens, J. Dejax, C. Denys, P. Duringer, V. Eisenmann, G. Fanone, P. Fronty, D. Geraads, T. Lehmann, F. Lihoreau, A. Louchart, A. Mahamat, G. Merceron, G. Mouchelin, O. Otero, P.P. Campomanes, M.P. de Leon, J.-C. Rage, M. Sapanet, M. Schuster, J. Sudre, P. Tassy, X. Valentin, P. Vignaud, L. Viriot, A. Zazzo & C. Zollikofer 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 418: 145-151.

Churcher, C.S. 1970. Two new Upper Miocene giraffids from Fort Ternan, East Africa; *Palaeotragus primaevus* n. sp. and *Samotherium africanum* n. sp. *Fossil Vertebrates of Africa*, 2: 1-105.

——— 1979. The large palaeotragine giraffid, *Palaeotragus germaini*, from late Miocene deposits of Lothagam Hill, Kenya. *Breviora*, 453: 1-8.

Cooke, H.B.S. 1987. Fossil Suidae from Sahabi, Libya. In (N. Boaz *et al.*, eds.) *Neogene Paleontology and Geology of Sahabi*, pp. 255-266. New York, Alan Liss.

Cooke, H.B.S. & R.F. Ewer 1972. Fossil Suidae from Kanapoi and Lothagam, northern Kenya. *Bulletin of the Museum of Comparative Zoology*, 143(3): 149-296.

Cooke, H.B.S. & Wilkinson, A.F. 1978. Suidae and Tayassuidae. In (V.J. Maglio & H.B.S. Cooke, eds.) *Evolution of African Mammals*, pp. 435-482. Harvard University Press, Cambridge.

Coppens, Y. 1994. East side story: the origin of humankind. *Scientific American*, May 1994: 88-95.

Gentry, A.W. 1978. Bovidae. In (V.J. Maglio & H.B.S. Cooke, eds.) *Evolution of African Mammals*, pp. 540-572. Harvard University Press, Cambridge.

——— 1990. Evolution and dispersal of African Bovidae. In (G.A. Bubenik & A.B. Bubenik, eds.) *Horns, Pronghorns, and Antlers. Evolution, Morphology, Physiology and Social Significance*, pp. 195-227. Springer-Verlag, New York.

——— 1999. Fossil pecorans from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In (P.J. Whybrow & A. Hill, eds.) *Fossil Vertebrates of Arabia*, pp. 290-316. Yale University Press, New Haven.

Ginsburg, L. 1977a. Les carnivores du Miocene de Beni Mellal. *Géologie Méditerranéenne*, 4(3): 225-240.

——— 1977b. L'Hyracoide (Mammifère sunongulé) du Miocène de Beni Mellal (Maroc). *Géologie Méditerranéenne*, 4(3): 241-254.

Ginsburg, L. & F. Chevrier 2001. Les Dinothères du bassin de la Loire et l'évolution du genre *Deinotherium* en France. *Symbioses*, 5: 9-24.

Golpe-Posse, J.M. 1979. Suidés des gisements du Bled Dourah (W de Gafsa, Tunisie). *Notes du Service Géologique de Tunisie*, 44: 75-107.

Hamilton, W.R. 1978. Fossil giraffes from the Miocene of Africa and a revision of the Phylogeny of the Giraffoidea. *Philosophical Transactions of the Royal Society of London, Series B*, 283(996): 165-229.

Harris, J.M. 1973. *Prodeinotherium* from Gebel Zelten, Libya. *Bulletin of the British Museum, Natural History (Geology)*, 23(5): 283-248.

——— 1978. Deinotherioidea and Barytherioidea. In (V.J. Maglio & H.B.S. Cooke, eds.) *Evolution of African Mammals*, pp. 315-335. Harvard Univ. Press, Cambridge.

Hendey, Q.B. 1974. The late Cenozoic Carnivora of south-western Cape Province. *Annals of the South African Museum*, 63: 1-369.

Hooijer, D.A. 1968. A rhinoceros from the late Miocene of Fort Ternan, Kenya. *Zoologische Mededelingen*, 43(6): 77-92.

Howell, F.C. 1987. Preliminary observations on Carnivora from the Sahabi Formation (Libya). In (N.T. Boaz *et al.*, eds.) *Neogene Paleontology and Geology of Sahabi*, pp. 153-181, Alan R. Liss., New York.

Ishida H. & M. Pickford 1997. A new Late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 325: 823-829.

Ishida, H., Y. Kunimatsu, M. Nakatsukasa, & Y. Nakano 1999. New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropological Science*, 107(2): 189-191.

Ishida H., Y. Kunimatsu, & M. Nakatsukasa 2001. Activities of the Samburu Hills/Nachola project in northern Kenya between 1998 and 2000. In (H. Ishida, ed.) *Study of Hominoid Evolution and Human Origin in East Africa. Research Papers of the Subsidy of Scientific Rresearch Funds during 1998-2000*, No. 10041164, pp. 3-58, the Ministry of Education, Science and Culture of Japan (unpublished).

Jacobs, L.L., J. Michaux & M. Sabatier 1980. Première données sur les rongeurs de la formation de Ch'orora (Ethiopie) d'âge Miocène supérieur, I. Thryonomyidaés. *Palaeovertebrata, Mémoire jubilaire en hommage à René Lavocat*, pp. 365-374.

Kalb, J.E., E.B. Oswald, S. Tebedge, A. Mebrate, E. Tola & D. Peak 1982a. Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. *Nature*, 298: 17-25.

Kalb, J.E., C.J. Jolly, A. Mebrate, S. Tebedge, C. Smart, E.B. Oswald, D. Cramer, P. Whitehead, C.B. Wood, G.C. Conroy, T. Adefris, L. Sperling & B. Kana 1982b. Fossil mammals and artifacts from the Middle Awash Valley, Ethiopia. *Nature*, 298: 25-29.

Kalb, J.E., C.J. Jolly, S. Tebedge, A. Mebrate, C. Smart, E.B. Oswald, D. Cramer, P. Whitehead, C.B. Wood, T. Adefris & V. Rawn-Schatzinger 1982c. Vertebrate faunas from the Awash Group, Middle Awash Valley, Afar, Ethiopia. *Journal of Vertebrate Paleontology*, 2(2): 237-258.

Kawamura Y. & H. Nakaya 1984. Thryonomyid rodent from the late Miocene Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 2: 133-139.

Kawamura Y. & H. Nakaya 1987. Additional materials of the late Miocene Rodents from the Namurungule Formation of Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 5: 131-139.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, San Diego.

Lavocat, R. Le gisement de vertébrés miocènes de Beni Mellal (Maroc). *Notes et Mémoires du Service Géologique (Rabat)*, 155: 1-120.

Leakey, L.S.B. 1958. Some east African Pleistocene Suidae. *Fossil Mammals of Africa*, 14: 1-133.

——— 1962. A new Lower Pliocene fossil primate from Kenya. *The Annals and Magazine of Natural History*, 13: 689-696

Le Gros Clark W.E. & L.S.B. Leakey 1951. The Miocene Hominoidea of East Africa. *Fossil Mammals of Africa*, 1: 1-117.

Lehman, U. & H. Thomas 1987. Fossil Bovidae from the Mio-Pliocene of Sahabi (Libya). In (N. Boaz *et al.*, eds.) *Neogene Paleontology and Geology of Sahabi*, pp. 323-335, Alan Liss, New York.

Leonardi, P. 1952. Resti fossili di *Sivachoerus* del giaccimento di Sahabi in Cirenaica (Africa Settentrionale). Notizie preliminari. *Atti della Accademia Nazionale dei Lincei, Rendiconti, Serie VIII*, 13: 166-169.

——— 1954. I suidi di Sahabi nella Sirtica (Africa Settentrionale). *Accademia Nazionale dei XL, Rendiconti, Serie IV*, 4: 75-88.

Meyer, G.E. 1978. Hyracoidea. In (V.J. Maglio & H.B.S. Cooke, eds.) *Evolution of African Mammals*, pp. 540-572, Harvard University Press, Cambridge.

Nakano, Y., H. Tsujikawa, H. Nakaya, M. Nakatsukasa, & H. Ishida 2001. The fossil footprints in Samburu Hills, Northern Kenya (in Japanese). *Africa Kenkyu*, 59: 101-114.

Nakaya, H. 1994. Faunal changes of late Miocene Africa and Eurasia: Mammalian fauna from the Namurungule Formation, Samburu Hills, northern Kenya. *African Study Monographs Supplementary Issue*, 20: 1-112.

Nakaya, H., M. Pickford, Y. Nakano & H. Ishida 1984. The late Miocene large mammal fauna from the Namurungule Formation, Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 87-131.

Nakaya, H., Pickford, M., Yasui, K. & H. Ishida 1987. Additional large mammalian fauna from the Namurungule Formation, Samburu Hills. *African Study Monographs Supplementary Issue*, 5: 79-129.

Nakaya H. & M. Watabe 1990. Hipparion from the Upper Miocene Namurungule Formation, Samburu Hills, Kenya: Phylogeny significance of newly discovered skull. *Geobios*, 23(2): 195-219.

Pickford, M. 1981. Preliminary Miocene mammalian biostratigraphy for western Kenya. *Journal of Human Evolution*, 10: 73-97.

——— 1983. On the origin of Hippopotamidae together with descriptions of two new species, a new subfamily from the Miocene of Kenya. *Geobios*, 16(2): 193-217.

——— 1986. A revision of the Miocene Suidae and Tayassuidae, (Artiodactyla, Mammalia) of Africa. *Tertiary Research Special Paper*, 7: 1-83.

——— 1988. Revision of the Miocene Suidae of the Indian Subcontinent. *Münchner Geowissenschaftliche Abhandlungen Reihe A*, 12: 1-92.

——— 1989. New specimens of *Nyanzachoerus waylandi* (Mammalia, Suidae, Tetraconodontinae) from the type area, Nyaburogo, (Upper Miocene), Lake Albert Rift, Uganda. *Geobios*, 22(5): 641-651.

——— 1990. Revision des Suidés de la formation de Beglia (Tunisie). *Annales de Paléontologie*, 76(2): 133-141.

——— 2001. *Afrochoerodon* nov. gen. *kisumuensis* (MacInnes) (Proboscidea, Mammalia) from Cheparawa, Middle Miocene, Kenya. *Annales de Paléontologie*, 87(2): 99-117.

——— 2004. Revision of the Early Miocene Hyracoidea (Mammalia) of East Africa. *Comptes Rendus Palevol*, 3(8): 675-690.

Pickford, M., H. Ishida, Y. Nakano & H. Nakaya 1984a. Fossiliferous localities of the Nachola-Samburu Hills Area, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 45-56.

Pickford M., H. Nakaya, I. Ishida & Y. Nakano 1984b. The biostratigraphic analyses of the faunas of the Nachola Area and Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 2: 67-72.

Pickford, M. & M.S. Fischer 1987. *Parapliohyrax ngororaensis*, a new hyracoid from the Miocene of Kenya, with an outline of the classification of Neogene Hyracoidea. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*,175(2): 207-234.

Pickford, M. & B. Senut 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 332: 145-152.

Rasmussen, D.T. & E.L. Simons 1988. New oligocene hyracoids from Egypt. *Journal of Vertebrate Paleontology*, 8(1): 67-83.

Savage, R.J.G. 1965. Fossil Mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum (Natural History) Geology*, 10: 239-316.

Sawada Y., M. Tateishi & S. Ishida 1987. Geology of the Neogene system in and around the Samburu Hills, Northern Kenya. *African Study Monographs Supplementary Issue*, 5: 7-26.

Sawada, Y., M. Pickford, T. Itaya, T. Makinouchi, M. Tateishi, K. Kabeto, S. Ishida & H. Ishida 1998. K-Ar ages of Miocene Hominoidea (*Kenyapithecus* and *Samburupithecus*) from Samburu Hills, Northern Kenya. *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 326: 445-451

Schmidt-Kittler, N. 1987. The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaeontographica Abteilung A*, 197: 85-126.

Senut, B., M. Pickford, D. Gommery, P. Mein, K. Cheboi & Y. Coppens 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie des Science, Series IIA, Sciences de la terre et des planètes*, 332: 137-144

Smart, C. 1976. The Lothagam 1 fauna: Its phylogenetic, ecological, and biogeographic significance. In (Y. Coppens, F.C. Howell, G.I. Isaac & R.E.F. Leakey, eds.) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 361-369. University of Chicago Press, Chicago.

Sotnikova, M.V. 1992. A new species of Machairodus from the Late Miocene Kalmakpai locality in eastern Kazakhstan (USSR). *Annales Zoologici Fennici*, 28(3-4): 361-369.

Tassy, P. 1986. Nouveaux Elaphantoidea (Mammalia) dans le Miocène du Kenya. *Cahiers de Paléontologie*, pp. 135. Éditions du Centre de la Recherere Scientifique, Paris.

Thomas, H. 1979. *Miotragocerus cyrenaicus* sp. nov. (Bovidae, Artiodactyla, Mammalia) du Miocène supérieur de Sahabi (Libye) et ses rapports avec les autres Miotragocerus. *Géobios*, 12(2): 267-281.

——— 1981. Les Bovidés miocènes de la formation de Ngorora du Bassin de Baringo (Rift Valley, Kenya). *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen, Series B, Palaeontology, Geology, Physics and Chemistry*, 84(3/4): 335-410.

Ward, S., B. Brown, A. Hill, J. Kelley & W. Downs 1999. *Equatorius*: A new hominoid genus from the middle Miocene of Kenya. *Science*, 285: 1382-1386.

White, T.D., G. Suwa, & B. Asfaw 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371: 306-312.

Whitworth, T. 1954. The Miocene hyracoids of East Africa, with some observations on the order Hyracoidea. *Fossil Mammals of Africa*, 7: 1-58.

———Accepted *March 31, 2005*

Author's Name and Address: Hiroshi TSUJIKAWA, *Laboratory of Physical Anthropology, Department of Zoology, Graduate School of Science, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto, 606-8052, Japan.*

E-mail: tsuji@anthro.zool.kyoto-u.ac.jp